



TITLE:

# STUDIES ON BENEFICIAL EFFECTS OF SILICON ON RICE PLANTS( Dissertation\_全文)

AUTHOR(S):

Ma, Jian Feng

---

CITATION:

Ma, Jian Feng. STUDIES ON BENEFICIAL EFFECTS OF SILICON ON RICE PLANTS. 京都大学, 1991, 農学博士

ISSUE DATE:

1991-03-23

URL:

<https://doi.org/10.11501/2964293>

RIGHT:

STUDIES ON BENEFICIAL EFFECTS OF  
SILICON ON RICE PLANTS

MA JIANFENG

1990

## CONTENTS

CHAPTER I	INTRODUCTION	1
CHAPTER II	CHARACTERISTICS OF SILICON IN RICE PLANTS	5
	Section 1. Significance of silica gel for rice growth	6
	Section 2. Formation process of silicified cells	11
CHAPTER III	POSSIBLE MECHANISM OF SILICON EFFECTS ON RICE GROWTH	21
	Section 1. Analysis of silicon effects on dry matter production and yield components	22
	Section 2. Possible mechanisms of silicon effects on dry matter production	26
	Section 3. Possible mechanism of silicon effects on yield components	36
CHAPTER IV	EFFECTS OF SILICON ON RICE GROWTH AT DIFFERENT GROWTH STAGES	41
CHAPTER V	INTERACTION BETWEEN SILICON AND PHOSPHORUS IN RICE PLANTS AND SOIL	55
	Section 1 Effect of Si on the growth and P uptake of rice plants at different P levels	55
	Section 2. Effect of silicic acid on P availability for rice plants in a P-deficient soil	64
	Section 3. Effect of silicate on P availability for rice plants in a P-deficient soil	75
CHAPTER VI	INTERACTION BETWEEN SILICON AND CALCIUM	84

CHAPTER VII	AVAILABILITY OF SILICA IN RICE STRAW FOR RICE	
PLANTS		91
Section 1. Availability of straw Si under no planting		92
Section 2. Availability of straw Si under rice planting		97
CONCLUSIONS		108
REFERENCES		110
LIST OF PUBLICATIONS		120
ACKNOWLEDGMENT		121

## CHAPTER I INTRODUCTION

Silicon (Si) is the second most abundant elements, either on the basis of weight or number of atoms, in the earth's crust. Because of its strong affinity, in nature Si always occurs in combination with other elements, particularly with oxygen and various metals. Si dioxide comprises about 60% of the earth's crust. Therefore, Si dioxide compounds are one of the most intensively studied groups of substances in chemistry (Rostow 1973).

Silica constitutes the framework of soils. In general, 60 to 80 % of soil is silica. It is not surprising, therefore that plants grown in soils contain Si in varying concentrations. However, because of its universal existence, earlier researchers paid little attention to the physiology and biochemistry of silica compounds. In 1862, Sachs, one of the early pioneers of plant nutrition studies, first asked the following question in his article on Si nutrition "...whether silicic acid is an indispensable substances for those plants that contain silica, whether it takes part in nutritional processes, and what is the relationship that exists between the uptake of silicic acid and the life of the plant?" (Sach 1862). Although a hundred years ago the methods of plant physiology and biochemistry were not well enough advanced to find a satisfactory answer to the questions that Sachs asked, his questions brought Si to the attention of plant nutrition researchers. Since then, many researchers have made studies on silicon nutrition in many plants, including rice, maize, wheat, sunflower, barley,



sugar beet, soybean, cucumber, tomato, oats, and so on. However, the results on Si essentiality are often various and contradictory with different plants and researchers. Even for the same plant species, Si beneficial effect has been recognized or not by different researchers.

Although there are some discrepancies on Si essentiality, or there are not sufficient evidences to prove Si as an essential element for higher plant if Arnon's criteria are used as the test of essentiality, there is no question that Si has a beneficial effect on rice growth according to numerous trials.

Rice plants usually contain 4 to 20% SiO<sub>2</sub> in dry weight, being a typical Si accumulators. Japanese researchers found that if the SiO<sub>2</sub> content in the rice straw is below 11% and/or the content of soil-available silicate (pH 4 ammonium acetate buffer solution soluble) is less than 10.5 mg per 100 g soil, rice yield responds significantly to silicate application. Since 1955, slag which is used as an acid soil amendment in America and Europe, has been applied as "silicate fertilizer" in Japan for increased rice production. For the same reason, silicate fertilizers are used in South Korea, Taiwan and more recently in China.

Beneficial effects of Si in the field have been ascribed to prevent lodging and fungal and insect attack, to improve posture for light interception and decrease mutual shading in the community (Takahashi 1987). Such mechanical effects are not direct physiological effects, but indirect effects of Si. Thus to clarify whether Si has physiological effects in rice plants or not, experiment is necessary to be carried out under conditions free from lodging, diseases and mutual shading. Okuda and Takahashi (1961) precisely cultured

rice plants using solution culture under the conditions described above. They found that both the dry weights of the shoots and the grains were increased by the addition of silicic acid. This fact suggested that Si may have physiological effects.

Numerous studies have been intensively made on Si in rice plant. Okuda and Takahashi (1962d), Takahashi and Hino (1978) found that rice plants absorb Si actively in the form of monosilicic acid. Si deposits as silica in leaf and stem after transported by transpiration stream, forming cuticle-silica double layers mainly in leaf blade (Yoshida *et al.* 1962a, b and c). More than 90 % of Si in rice plants is present in the form of silica gel, and Si is immobile in the plant (Yoshida 1962d). Si promotes the oxidation power of root, resulting in decreasing Fe and Mn uptake (Okuda and Takahashi 1962a, b). Si effects appear larger under the conditions of higher levels of nitrogen and phosphorus, lower levels of phosphorus (Ishizuka *et al.* 1958, Okuda and Takahashi 1962c, Tanaka 1980). Okuda and Takahashi (1961) reported that the effect and uptake of Si are larger when Si is added at later growth stage (after panicle initiation stage) than at earlier growth stage. Si increases the resistance of rice plant to stress such as radioactivity and salt (Takahashi 1966, Matoh *et al.* 1986).

As described above, many facts on Si effects in rice plants have been obtained, however, the physiological roles of Si in rice plants have not been well understood yet. Even now, we can not give a definitive answer to the questions that Sachs asked.

In the present study, I try to find some new facts on Si in rice plants and to clarify the mechanisms of Si effects that has been found. In Chapter II, I make the following questions clear: why Si has no excess damage, which form of Si in rice plants is the most important for growth and how to form silicified cells. I present the possible mechanisms of Si effects on dry matter production and yield components, respectively, in Chapter III. For economical and effective application of new silicate fertilizers, Si effect at different growth stages is studied in Chapter IV. In Chapter V, detailed researches on the interaction between P and Si are made in terms of uptake and chemical reaction in soil, respectively. I also discuss in Chapter VI the interaction between Si and Ca which often accompanies Si when silicate fertilizers (mainly calcium silicate) are applied. Finally, in Chapter VII, considering Si recycling, I study the availability of Si in rice straw for rice plants.

## CHAPTER II CHARACTERISTICS OF SILICON IN RICE PLANTS

Rice plant has an adequate range of each essential element for healthy growth. Below or over this range, rice plant will appear deficient or excess symptoms, and the growth will be inhibited. However, There have not been any reports on Si excess damage yet. Why Si has no Si toxicity is a very interesting fact.

Based on the reactivity with molybdate and physiological state, Yoshida *et al.* (1962d) fractionated Si in the rice plant into three forms, namely silicate ion, colloidal silicic acid and silica gel. He found that silica gel constitutes more than 90 % of the total Si in the rice plant. However, it is not yet clear how Si forms change with growth progression, how much is the concentration of Si in the cell sap, and which form is the most important for rice growth.

On the other hand, silica gel deposits mainly in the leaf blade, forming silicified cells (Yoshida 1962c). However, when the SiO<sub>2</sub> content of the shoot was below 5%, the silicified cells could not be observed in the leaf blades (Yamazaki 1966). It is interesting to know the forms of Si in the rice plant below this content, and the process of silicified cell formation for understanding the behavior of Si in the rice plant. In this chapter, several experiments were conducted to make the above questions clear.

## Section 1. Significance of silica gel for rice growth

### MATERIALS AND METHODS

#### Change of Si forms with growth progression.

Water culture was used. The base nutrient solution for this and other studies was Kimura B solution. It has the following composition in *mM* : 0.37  $(\text{NH}_4)_2\text{SO}_4$ , 0.18  $\text{KNO}_3$ , 0.21  $\text{KH}_2\text{PO}_4$ , 0.37  $\text{Ca}(\text{NO}_3)_2$ , 0.55  $\text{MgSO}_4$ ,  $9.0 \times 10^{-2}$  EDTA-Fe,  $7.3 \times 10^{-3}$   $\text{MnSO}_4$ ,  $9.3 \times 10^{-3}$   $\text{H}_3\text{BO}_3$ ,  $1.6 \times 10^{-4}$   $\text{CuSO}_4$ ,  $1.5 \times 10^{-5}$   $(\text{NH}_4)_6\text{Mo}_2\text{O}_{24}$  and  $1.5 \times 10^{-4}$   $\text{ZnSO}_4$ .

Rice seeds (*Oryza sativa* L. cv. Akebono) were soaked in distilled water for two days and then sown in a plastic tray containing acid washed polyethylene beads as rooting media. After two weeks, the distilled water was exchanged for 1/4 strength Kimura B nutrient solution. After one more weeks, seedlings were transplanted into 1/2 strength Kimura B solution. The solution was renewed once a week. After 3 more weeks, three seedlings each were transplanted into 3 liter pots with full strength Kimura B solution containing 100 ppm  $\text{SiO}_2$  as silicic acid prepared by the Okuda and Takahashi method (1961a) in three replicates. The solution was adjusted to about pH 5.5 with 1 N KOH and renewed every day. Samples of the shoot for Si fractionation were taken on the day of 1, 2, 3, 5, 8, 11 and 15. The experiment was conducted in a green house. The method of Si fractionation in the shoot was the same as

suggested by Yoshida *et al.* (1962d). The fresh samples were cut into fragments, and separated into two parts, one for total Si and the other for silicate ion and colloidal silicic acid determination. The total content of Si was determined by the colorimetric molybdenum blue method after the samples were melted with  $\text{Na}_2\text{CO}_3$ . The methods for determination of silicate ion and colloidal silicic acid are described as following. Five gram of fresh sample was homogenized with 50 ml of distilled water using a mixer for 3 min. The homogenate was filtered through a gauze into 100 ml flask to which 1 ml of 0.2 N HCl was added to minimize the rate of possible transformation of silicic acid, both polymerization and depolymerization. After filled up, the content was transferred to a centrifugal tube and centrifuged at 5000 r.p.m. for 10 min. and filtered through a dry filter paper. The filtrate was separated into two parts, one for silicate ion determination and the other for colloidal silicic acid plus silicate ion determination. The content of silicate ion was determined immediately by the colorimetric molybdenum blue method. The colloidal silicic acid plus silicate ion was measured by the same method after melted with  $\text{Na}_2\text{CO}_3$ .

#### Si concentration in the cell sap

The culture method was the same as described above. After rice plants were treated with silicic acid (100 ppm  $\text{SiO}_2$ ) for three weeks, samples of rice shoots were taken at 12:00 and 17:00 in three replicates. The samples were freezed by liquid nitrogen immediately, and then the sap was taken. The concentration of Si in the sap was determined by the colorimetric method.



### Significance of silica gel for rice growth

Rice seedlings grown for two weeks were treated with 20 and 100 ppm  $\text{SiO}_2$  as silicic acid in green house. The rice plants were cultured in the same method as described above in three replicates. After 4 weeks, rice plants were harvested. The dry weight of the shoot was measured and the Si in the leaf blades was fractionated using the method described above.

## RESULTS

Because the content of silicate ion and colloidal silicic acid in the shoot was very low, the sum of both was shown in Fig. 1. Total Si content increased with the progression of rice growth, from 2.5 %  $\text{SiO}_2$  on the first day after silicic acid supply to 14 %  $\text{SiO}_2$  in dry weight at the end of the experiment. The content of silica gel increased in the same trend as the total silicon. The content of silicate ion and colloidal silicic acid ranged from 300 to 500 ppm  $\text{SiO}_2$  regardless of the growth progression. Silica gel constituted more than 90 % of the total Si at any time and Si content.

The concentration of Si in the sap was about 160 ppm  $\text{SiO}_2$  either at noon or in the evening (Table 1).

Table 1 The concentration of Si in the cell sap of rice plant.

Values are means (n=3) with SD in the parenthesis

Time	12:00	16:00
Conc. ( $\text{SiO}_2$ ppm)	157.5 (27.1)	172.5 (23.2)

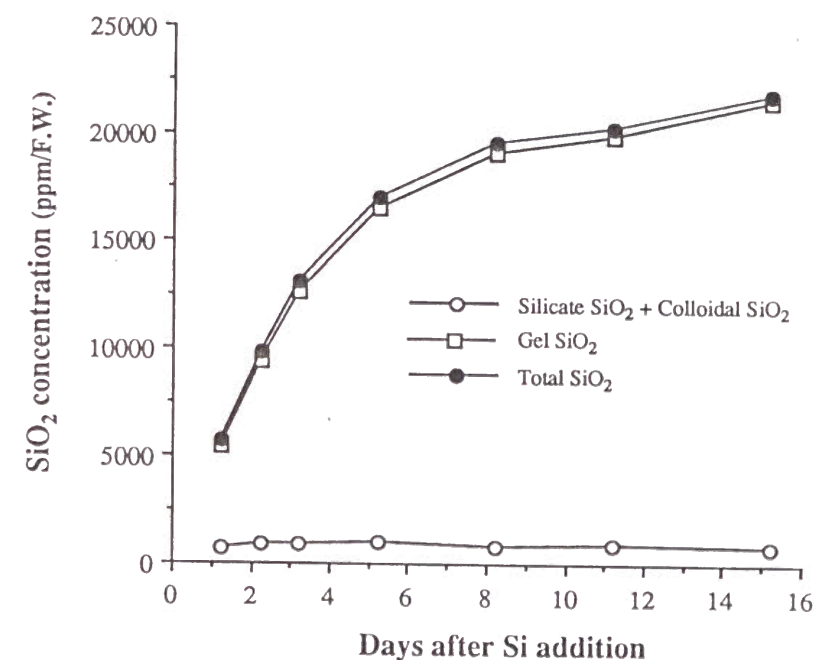


Fig. 1 Changes of Si forms in rice plants with the growth progression

Compared to the rice plants treated with 20 ppm  $\text{SiO}_2$ , the rice plants treated with 100 ppm  $\text{SiO}_2$  increased dry weight of the shoots 11 % (Table 2).

The rice plants with 100 ppm contained about 4 times as much both total silicon and silica gel in the leaf blades as the plants with 20 ppm. However, the total of silicate ion and colloidal silicic acid in the leaf blades hardly changed between the treatments.

*Table 2* Dry weight of the shoot and Si forms in the leaf blade at different Si levels

SiO <sub>2</sub> level (ppm)	Shoot dry weight (g)	Si forms (SiO <sub>2</sub> ppm/F.W.)			
		Ionic	Colloidal	Gel	Total
20	10.1	73.4	74.1	3,593	3,740
100	11.2	126.2	27.3	13,685	13,838

## DISCUSSION

Above three experiments revealed that although the content of silicate ion and colloidal silicic acid had little fluctuation with Si supply levels and time, total of both retained below 500 ppm as SiO<sub>2</sub> either in the leaf blade and the shoot or in the cell sap (Fig. 1, Table 1, 2). Silica gel is the most prevalent form of silicon. With Si accumulating in the shoot, silica gel also increased correspondingly.

As stated in the introduction, rice plant absorbs Si in the forms of monosilicic acid (Takahashi and Hino 1978). Above facts suggest that the concentration of silicate ion and/or colloidal silicic acid is over 500 ppm SiO<sub>2</sub>, the Si will gel. It may be the reason why Si has no excess toxicity in rice plant

even accumulated up to 20 % SiO<sub>2</sub> in dry weight. Because of its polymerization, Si does not inhibit enzyme reactions and create abnormal osmotic pressure.

Dry weight of the shoots increased with increasing Si supply levels (Table 2). However, the concentration of silicate ion and colloidal silicic acid did not change much compared the rice plants containing 4 % SiO<sub>2</sub> in dry weight with those containing 15 % SiO<sub>2</sub>. Therefore it is difficult to image that Si takes part in any biochemical actions. If this is so, perhaps only little Si will be enough for the growth, also there will not be difference in the dry weight of the shoots between above two rice plants containing different Si. It is evident that silica gel is the most important form of Si in rice plants. The roles of silica gel will be discussed in other sections and chapters.

## Section 2 Formation process of silicified cells

It is clear in the section 1 that Si polymerized even when the Si content of the shoot was below 5 % SiO<sub>2</sub> (Fig. 1). However, silicified cells could not be observed below this content (Yamazaki 1966). In this section, the process of silicified cells formation and the relationship between Si content and silicified cells are discussed.

## MATERIALS AND METHODS

### Histochemistry method

Rice seedlings were grown in Kimura B solution without Si for 4 weeks in the same method as described in section 1. Two seedlings each were then transplanted into 3 liter pots with supplied 100 ppm SiO<sub>2</sub> as silicic acid daily in three replicates. On the day of 1, 2, 3, 5, 8, 11 and 15 after Si supply, samples were taken for Si determination and silicified cells observation. Si content of the shoot was determined by the method described in the section 1. The second and third leaf blades (numbered from the top) were used for silicified cells observation. After chlorophyll of the leaf blades was removed by immersing them in 60 % alcohol, leaf blades were cut into every 2 cm, and then boiled in 70 % phenol solution with safranin for several minutes (Yamazaki 1966). The silicified cells at 2-4 cm, 6-8 cm, 8-10 cm and 14-16 cm in leaf blades were observed and measured with a light microscope. For each sample, 15 views were replicated. Rice plants without Si were also analyzed as control.

### Soft X-ray irradiation method

This method was developed by Takeoka *et al.* (1983). It based on a fact that amorphous silica gel absorbs X-ray energy more markedly than epidermal tissues do, causing more clear transparency on the developed X-ray film.

Rice seedlings of 20 days age were cultured in the solution with and without 20, 100 ppm SiO<sub>2</sub> for 5 weeks in four replicates using the same culture method

as described above. The third leaf blade was taken for soft X-ray irradiation. After the leaf blade was dried by an iron, it was irradiated on enclosed soft X-ray film by the microsource of X-rays, CMR, emitted by the SOFTEX machine (Model M1005NA), using under 8 KeV, 5 mA for one minute. The films were developed and made into photographs.

## RESULTS AND DISCUSSION

Two kinds of silicified cells were observed under light microscopy (Fig. 2). One was on the leaf vein, and the other between veins. The former was named silica cell, and the latter silica body or silica motor cell in this study. The silica cells formed on vascular bundles, and the silica bodies in bulliform cells of rice leaves. When Si content of the shoot was below 5 % SiO<sub>2</sub>, silica cells were found, but silica bodies hardly could be (Fig. 2b). With increasing the Si content, silica bodies increased (Fig. 2 c,d). It suggests that the formation process of silicified cells is from silica cells to silica bodies. This fact also suggests that the number of silica bodies can reflect the degree of Si accumulation.



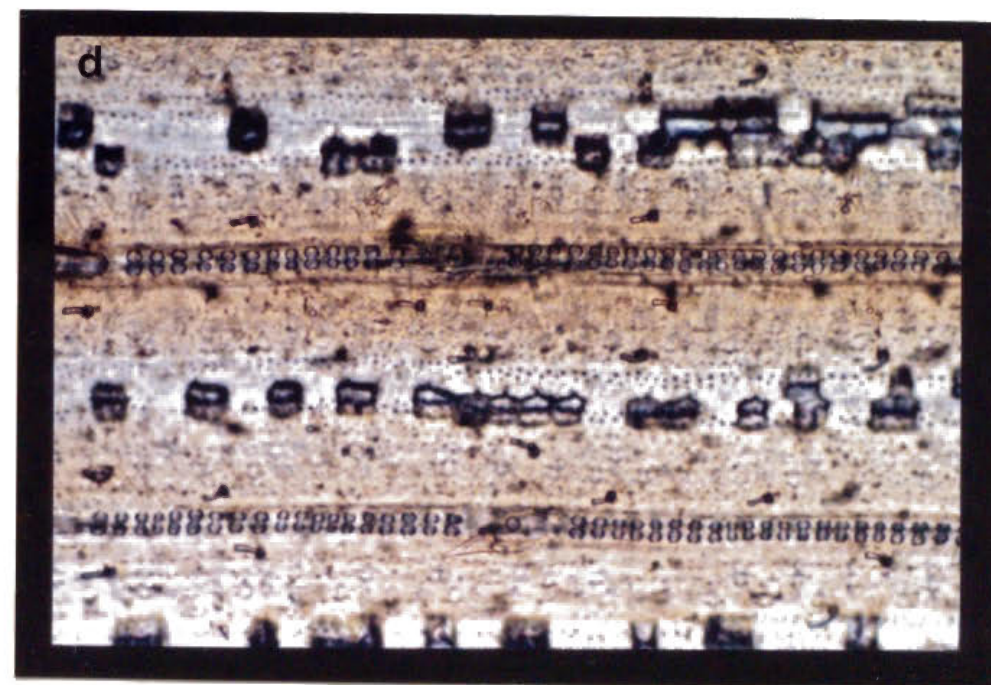
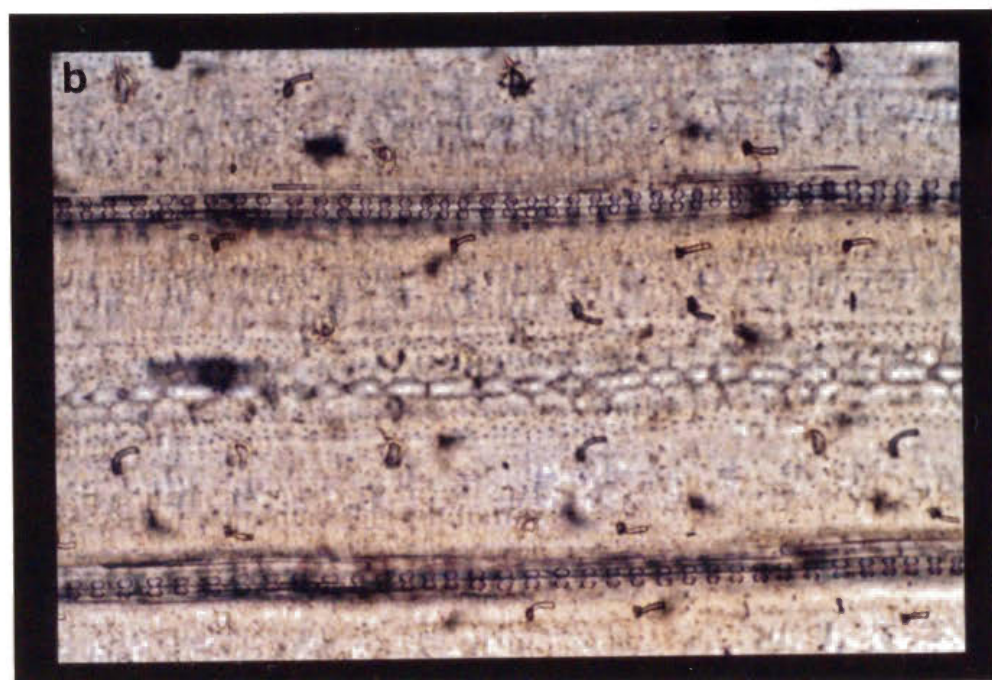


Fig. 2 Formation process of silicified cells in rice leaf blades (cv. Akebono).



(continued) The range between 8 and 10 cm from the tip was examined under light microscope. Allx100. a. The Si content of the shoot is 0.11 %  $\text{SiO}_2$ , showing no silicified cells. b. the Si content is 4.07 %, showing silica cells on the vein. c. The content is 8.75 %, showing silica cells and few silica bodies. d. The content is 10.5 %, showing silica cells and many silica bodies.

The relationship between silica bodies and Si contents is shown in Fig. 3. When Si content of the shoots was below about 5 %  $\text{SiO}_2$ , the numbers of silica bodies in the leaf blades were below 10 in 1  $\text{mm}^2$  at any position, and did not increase much with increasing the Si content. However, when the Si content became above 5 %  $\text{SiO}_2$ , the silica bodies increased significantly with the Si content. The silica bodies in the different leaf positions and distances showed the same trends as above.

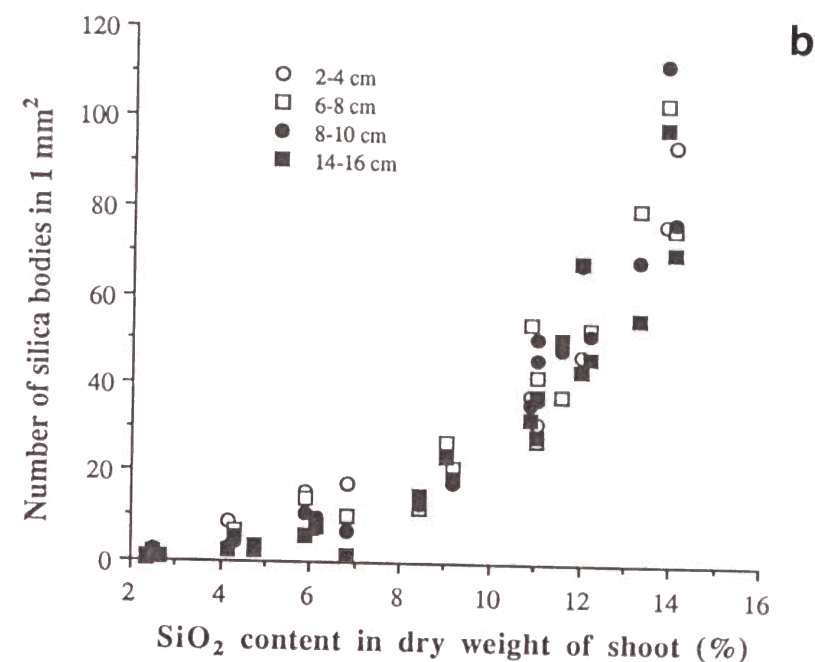
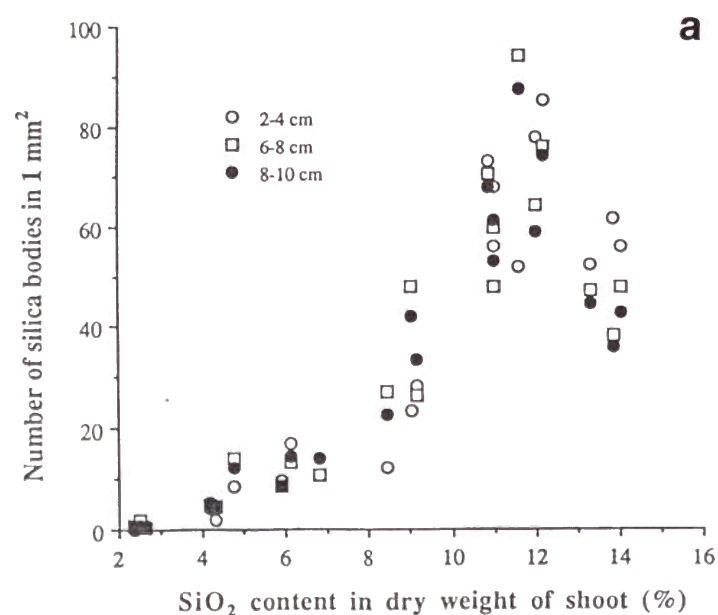


Fig. 3. Relationship between silica bodies in the leaf blades and Si content of the shoot. a and b show the silica bodies in the second and third leaf blades, respectively. Legends such as 2-4 cm represent the distance from the tip of the leaf blade. The numbers of silica bodies are the means of 15 views each of three leaf blades (n=45).

Microphotograph of a selected portion of the leaf blade obtained by soft X-ray irradiation clearly shows the silica bodies in the leaf blade (Fig. 4). The numbers of silica bodies in 1  $\text{mm}^2$  was 0, 4, 61 in the leaf blades which contained 0.12, 3.2, 11.3 %  $\text{SiO}_2$ , respectively.



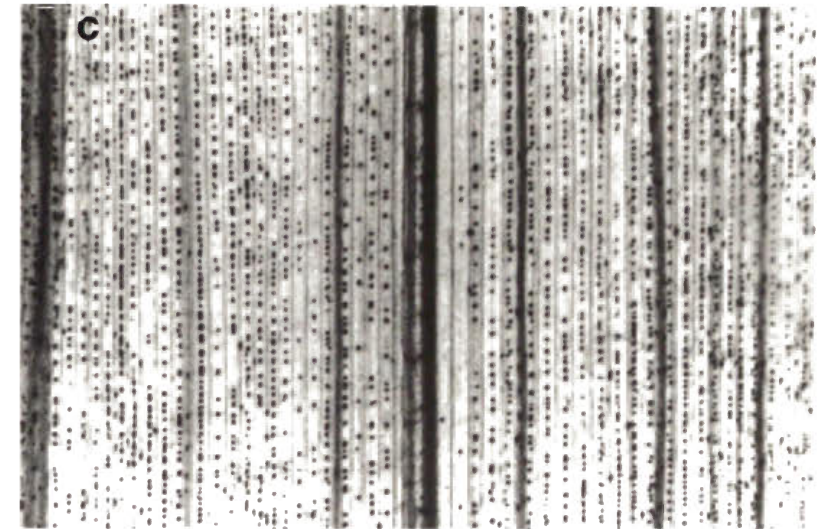
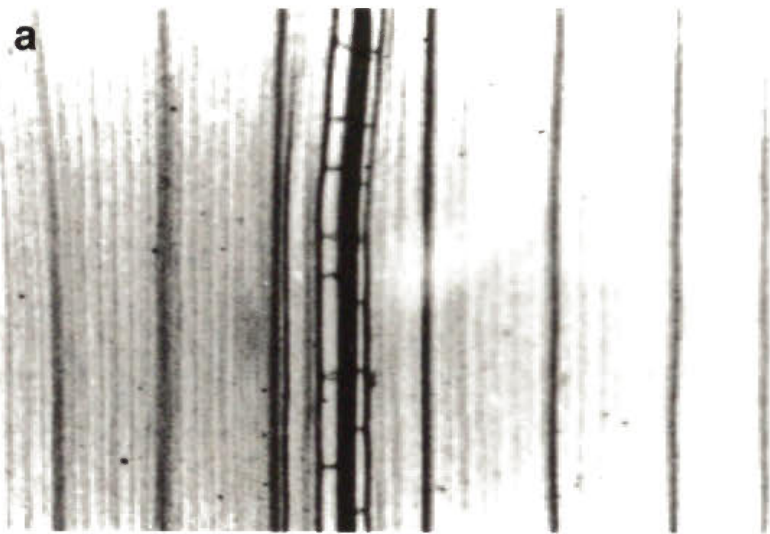
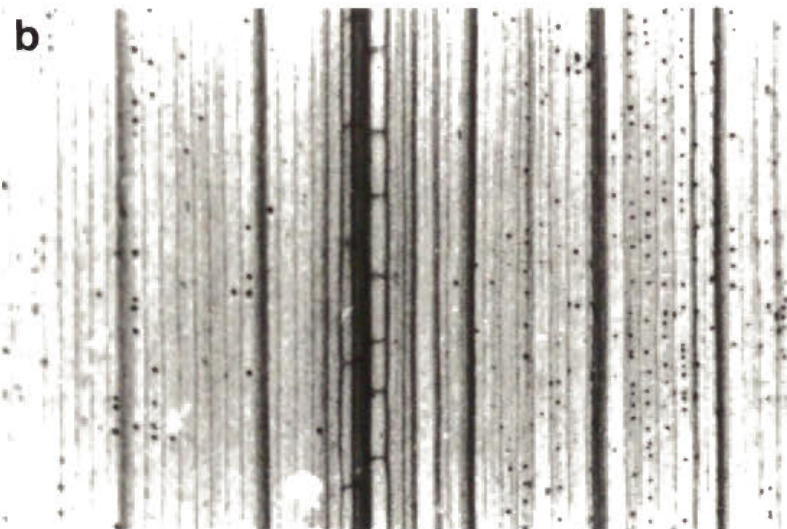


Fig. 4. Microphotograph obtained near 10 cm of leaf blade, showing no (a), few (b) and many silica bodies (c), respectively. The rice cultivar is "Akebono". Allx15.



It is evident from the above experiments that it was a wrong conclusion that cells could not be silicified when the content of Si in the shoot was below 5 %  $\text{SiO}_2$  (Yamazaki 1966). Below this content, cells are also silicified, but silica bodies hardly form (Figs. 2, 3). This phenomenon may be related to the transpiration. In addition to leaf blades, silicified cells were also observed in the epidermis and vascular tissues of stem, leaf sheath and hull *etc.* These silicification contributes to increasing the strength and rigidity of cell walls, thus increasing the resistance of rice plants to diseases and lodging, improving light-receiving plant form in community, and decreasing transpiration, *etc.*

It is clear that silica gel deposited in the shoot as silica cells and silica bodies plays the most important role in affecting rice growth. The physiological roles will be discussed in the next chapter.

### CHAPTER III POSSIBLE MECHANISMS OF SILICON EFFECTS ON RICE GROWTH

How does silica gel deposited in the rice plants affect their growth in addition to the mechanical effects? This question has not been well understood yet. There are two hypothesizes, one is named as "excess transpiration control", which was proposed by Takahashi (1987), and the other is "window theory" by Kaufman (1979). Takahashi (1987) indicated that silica decreases excess water loss from the leaf surface. If the deposition of silica is insufficient, excessive water loss may induce water stress in the leaf blades. Water stress may cause drooping of the leaf blades and the closure of stomata and thus suppression of CO<sub>2</sub> uptake.

On the other hand, Kaufman (1979) suggested that silicified cells might serve as a "window" in the epidermal system of sugarcane, and they may allow light to be transmitted to the photosynthetic mesophyll tissue below the epidermis better. Rice plants contain a higher content of Si and more silicified cells than sugarcane. It can be supposed that silica may promote photosynthesis by improving light transmission through the silicified cells also in rice plants if the hypothesis is true.

Although above hypothesizes are based on the fact that silica deposits on the epidermal of leaf blades, there has not yet been any direct evidence to support the both. In this chapter, the possible mechanisms of Si effects on rice

plants are discussed.

## **Section 1 Analysis of silicon effects on dry matter production and yield components**

In this section, the Si effects on dry matter production and yield components were examined, respectively, for the sake of convenience to discuss the possible mechanisms in the following sections.

## **MATERIALS AND METHODS**

Rice seedlings grown in 1/4 strength Kimura B solution for 25 days were used in the experiment. On June 10, 1986, three selected seedlings each were transplanted into the pots with Kimura B solution contained no Si or 100 ppm  $\text{SiO}_2$  as silicic acid (+/- Si treatments). The pots were arranged on greenhouse tables in a completely randomized design in 3 replications. The strength of the nutrient solution was modified with the progression of growth from 1/4 to 2 times, and pot sizes were also changed correspondingly. Distilled water with a copper still was used for the experiment. The solution was renewed once a week in the earlier period, and once three days in the later period. The pH of the solution was adjusted to about 5.5 with 0.5 N KOH.

The heading time was Oct. 2, and on Nov. 15, all the plants were harvested. Each plant was separated into panicles, leaf blades, stems

(culm+leaf sheath) and roots. After measuring the dry weights and yield components, the samples were used for the determination of Si content by the method described above. The percentage of filled spikelets was measured by a salt solution with a specific gravity of 1.06. Transpiration was measured by weighing the pots before and after the solution renewal throughout the whole growth period.

## **RESULTS AND DISCUSSION**

The +Si treatment did not increase the dry weight of the root (Table 3). The dry weights of the shoot and the grain increased about 1.25 and 2.5 times, respectively, with Si addition. After deducing  $\text{SiO}_2$  from the +Si plants, the dry weight of the shoot was 10 % more than that of -Si plants.

The -Si treatment decreased the panicle number and spikelet number per panicle 10 to 20 percent compared to +Si treatment (Fig. 5). The 1000-grain weight was hardly affected. However, the percentage of filled spikelets in the -Si treatment was nearly half of that in the +Si treatment.

Due to silicic acid addition, the Si content of leaf blade reached as high as 17 %  $\text{SiO}_2$ , and that of the hull followed (Table 4). The Si content of rice plants without Si was controlled below 0.4 %  $\text{SiO}_2$ . The small amount of Si in the -Si rice plants may be caused by silicious dust. Transpiration increased 30 % in the -Si plants (Table 5).



Table 3 Dry weights of grains and different parts of rice plants grown in the solution with and without silicic acid

	Leaf blade	Stem	Root (g)	Shoot <sup>a</sup>	Gain
+Si	47.3	82.2	12.1	129.5	27.7
-Si	40.3	63.3	13.9	103.6	11.2
+Si/-Si	1.17	1.30	0.87	1.25	2.47
After deducing SiO <sub>2</sub>					
+Si	39.3	74.6	11.8	113.9	
-Si	40.2	63.3	13.9	103.5	
+Si/-Si	0.98	1.19	0.85	1.10	

<sup>a</sup> excepting the panicles.

Table 4 Si content (% SiO<sub>2</sub>) in plant parts treated with and without silicic acid.

Treatment	Leaf blade	Stem	Shoot	Hull	Root
+Si	16.96	9.21	12.04	15.20	2.07
-Si	0.20	0.03	0.10	0.38	0.04

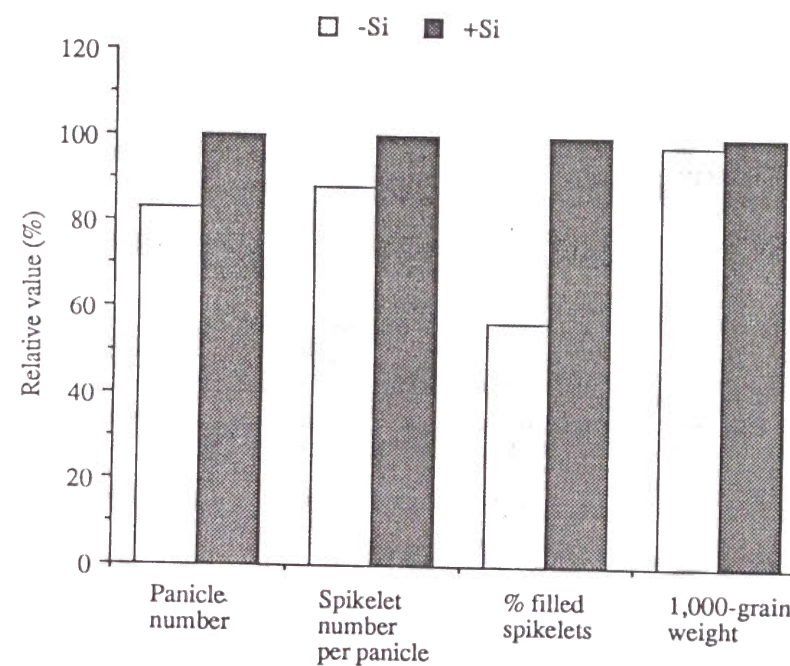


Fig. 5 Effect of Si on the yield components of rice plant. Data are relative values of +Si treatment (as 100).

Table 5 Transpiration of rice plants with and without Si

Transpiration (H <sub>2</sub> O g/D.W. g)	
+Si	-Si
506.8	662.9
(100)	(131)

The beneficial effects of Si on rice growth were also obtained in this

experiment as reported by Takahashi (1961b) and many other researchers (Table 3). The results clearly show that Si affect the percentage of filled spikelets more than dry matter production (Table 3, Fig. 5). It seems that Si may have different mechanisms in affecting dry matter production and the percentage of filled spikelets although the both have close relation. The possible mechanisms are separately discussed in the following sections.

## **Section 2 Possible mechanisms of silicon effects on dry matter production**

As introduced above, there have been two hypothesizes on Si promoting photosynthesis. In this section, the possibility of the both is discussed.

Before experiments, the following inferences are made. If the "window theory" is correct, the Si effect will show larger under weak light range than strong light range. If the "excess transpiration control" is true, Si effect will appear more under the conditions of high transpiration such as low relative humidity, high temperature than those of low transpiration (high relative humidity, low temperature). In this section, Si effects under different conditions were examined.

## **MATERIALS AND METHODS**

**Exp.1** Rice seedlings were grown for 3 weeks in the 1/2 strength Kimura B

solution without silicon, and then three seedlings each were transplanted into 3 liter pots with full strength Kimura B solution. -/+Si treatments were made in three replicates. +Si treatment was supplied 100 ppm SiO<sub>2</sub> as silicic acid. The culture method was the same as described above. On the day of 20, 30 and 40 after +Si treatment, the rate of CO<sub>2</sub> assimilation and transpiration, and leaf conductance were measured simultaneously by an equipment manufactured by Shimadzu (SPB-H2 type) (Hatamoto 1987). The measurement was conducted each thirty minutes near the 10 cm of the second leaf numbered from the new leaf from A.M. 6:00 to P.M. 5:00 in a green house. The same leaves were also measured under the conditions of 30°C and 30% (relative humidity) in a growth chamber. All plants were harvested on 45 day after treatments, and the dry weight of the shoot and Si content were determined.

**Exp.2** Twenty days seedlings were treated with and without 100 ppm SiO<sub>2</sub> as silicic acid for 26 days in the same method described above in four replicates. On the days indicated in figure, fresh weights of whole plants were measured.

**Exp. 3** Flowing water culture was used in this experiment. The strength of the solution was 1/10 of Kimura B, and the concentration was adjusted every day. The flowing rate of the solution was 2 liter per 1 minute. Four seedlings each of 25 days age were transplanted into one unit. The units were arranged on green house tables in a completely randomized design with +/-Si main treatments and shading or no shading subtreatments. The light-interception coefficient for

shading treatment was 52 %, and +Si treatment was supplied 20 ppm SiO<sub>2</sub> every day as silicic acid. The treatments were continued for 20 days.

**Exp. 4** Three seedlings each of 17 days age were treated with and without silicic acid in 1 liter pots with Kimura B solution. The plants were cultured for ten days after treatment in a growth chamber under the conditions of 30°C, RH: 40±15%. The same seedlings were cultured for one month under the conditions of 30°C, RH: 90±15%. The photo flux density of both conditions was about 350  $\mu\text{mol}/\text{m}^2/\text{sec}$ . The culture method was the same as described above.

**Exp. 5** The same seedlings used in Exp. 3 were treated with and without silicic acid for 20 days in three replicates. The leaf blades of half of -Si plants were supported by wires to improve light-receiving form as same possible as +Si plants. The culture method was the same as described in the Exp. 3.

## RESULTS

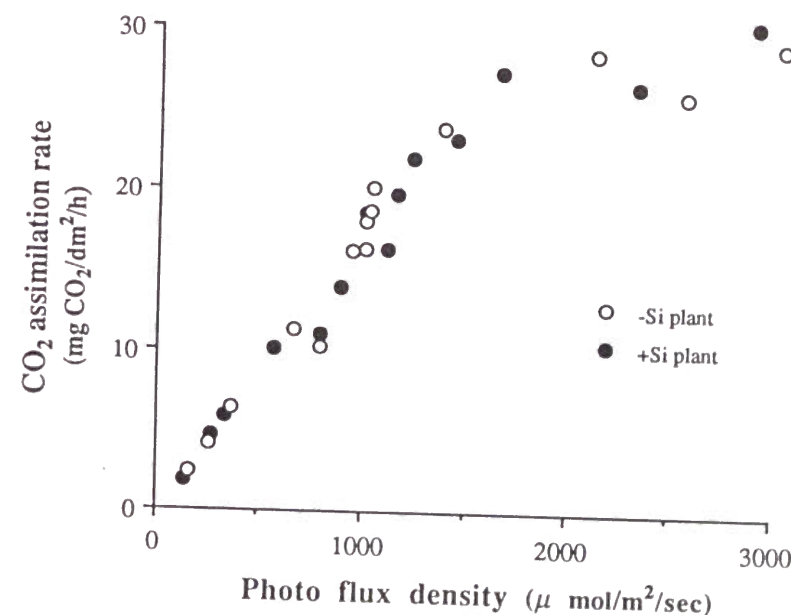
The dry weight of the +Si shoots significantly increased compared to the -Si shoots at harvest (Table 6). The Si content in the +Si shoots was 10.1 % SiO<sub>2</sub>, and that in the -Si shoots was 0.1 %.

Measurement of the photosynthesis was conducted at different days as indicated in the Materials and Methods. Since the same trends were obtained, selected example is shown in Fig. 6. The rate of CO<sub>2</sub> assimilation responded

significantly to photo flux density up to 1700  $\mu\text{mol}/\text{m}^2/\text{h}$  in either -Si plants or +Si plants. The difference in the CO<sub>2</sub> assimilation rate between -Si and +Si plants was not obtained under any photo flux density.

*Table 6* Dry weight and Si content of the rice shoots treated with and without 100 ppm SiO<sub>2</sub> as silicic acid for 45 days. Values are means(n=3) with SD within brackets to right

Treatment	Shoot dry weight (g/pot)	Shoot Si content (SiO <sub>2</sub> %)
-Si	18.30 (0.48)	0.11 (0.06)
+Si	22.67 (1.07)	10.12 (0.36)



*Fig. 6* Effect of Si on light response curves of CO<sub>2</sub> assimilation rate.

Results measured under the condition of higher transpiration show that the rate of CO<sub>2</sub> assimilation and transpiration, and leaf conductance did not significantly increased in the + Si plants (Table 7).

*Table 7* Effect of Si on the rate of CO<sub>2</sub> assimilation and transpiration, and leaf conductances under the condition of higher transpiration conducted in the growth chamber and green house, respectively. Values are means (n=9) with SD within brackets in right.

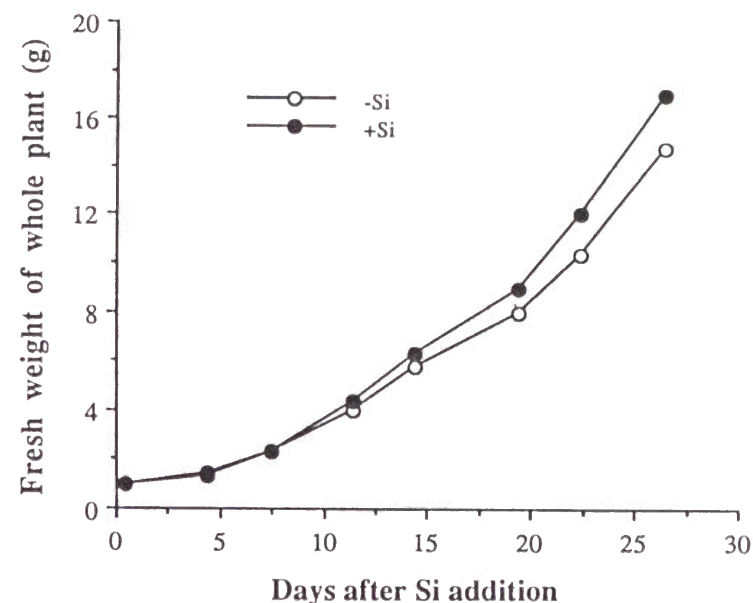
Treatment	CO <sub>2</sub> assimilation rate (mg CO <sub>2</sub> /dm <sup>3</sup> /h)	Transpiration rate (mgH <sub>2</sub> O/dm <sup>3</sup> /h)	Leaf conductance (cm/s)
In green house <sup>a</sup>			
-Si	25.49 (3.39)	7,805 (379)	1.16 (0.17)
+Si	26.01 (4.02)	7,211 (340)	1.00 (0.22)
In growth chamber <sup>b</sup>			
-Si	3.67 (0.95)	5,630 (518)	1.80 (0.66)
+Si	3.84 (0.65)	5,825 (516)	1.93 (0.57)

<sup>a</sup> measured in the green house at PM 1:00 under the condition of 36°C, RH: 40±10% and 2800  $\mu$  mol/m<sup>3</sup>/sec.

<sup>b</sup> measured in the growth chamber under the condition of 30°C, RH: 30±15% and 350  $\mu$  mol/m<sup>3</sup>/sec.

The differences in fresh weights between - Si plants and +Si plants became

bigger and bigger with the progression of growth (Fig. 7). During initial days after treatment, Si hardly increased the fresh weights, however, at the end of the experiment, Si increased the fresh weight about 15 %.



*Fig. 7* Changes of Si effect on the fresh weight of rice plants with progression of the growth.

With shading treatment, the fresh weight ratio of +Si to -Si was larger compared to no shading (Table 8). Dry weight of the shoot was significantly increased, and the transpiration rate was decreased by Si treatment under the condition of 40 % RH (Table 9). However, the same trends were not obtained under the condition of 90% RH.



*Table 8* Effect of Si on the fresh weight of rice shoot treated with shading or not. Values are means (n=4) with SD in parentheses.

Treatment	No shading	Shading
	(g/pot)	
-Si	3.76 (0.27)	1.45 (0.04)
+Si	4.14 (0.10)	2.03 (0.08)
+Si/-Si	1.10	1.40

*Table 9* Effect of Si on dry weight of rice shoots, transpiration rate under different humidities. Values are means (n=4) with SD in parentheses.

Treatment	Shoot dry weight (g/pot)	Transpiration rate (H <sub>2</sub> O g/D.W. g)
RH: 40 % <sup>a</sup>		
+Si	0.91 (0.06)	471.1 (28.7)
-Si	0.73 (0.04)	635.9 (21.4)
+Si/-Si	1.25	0.74
RH: 90% <sup>b</sup>		
+Si	4.40 (0.18)	297.6 (3.5)
-Si	4.05 (0.21)	323.3 (8.5)
+Si/-Si	1.09	0.92

<sup>a</sup> grown for 10 days.

<sup>b</sup> grown for 30 days.

The fresh weight of -Si rice shoots was increased by changed light-receiving forms using wires (Table 10).

*Table 10* Fresh weight of rice shoots treated with Si or not, and with changed light receiving plant form. Values are means (n=3) with SD in parentheses.

Treatment <sup>a</sup>	Shoot fresh weight (g/pot)
-Sia	4.01 (0.18)
-Sib	3.51 (0.05)
+Si	4.02 (0.02)

<sup>a</sup> -Sia and -Sib represent the treatments of changed light-receiving plant form or not by supporting leaf blades using wires, respectively, under no Si supply.

## DISCUSSION

The light saturation point of rice plant is 830 to 1100  $\mu$  mol/m<sup>2</sup>/sec. (45 to 60 klx) at 30°C, 300 ppm CO<sub>2</sub> (Murata 1961). As stated above, if the "window theory" is correct, Si will increase the CO<sub>2</sub> assimilation rate when light intensity is below this point. However, in this experiment, as shown in the Fig. 6, the results to support this hypothesis could not be obtained. Under the condition of low humidity, the effect of Si on the photosynthesis was also expected, but any difference between -Si plants and +Si plants in photosynthesis, transpiration



and leaf conductance could not be found (Table 7). Kawamitsu *et al.* (1989) reported the same results.

It is unaccountable that the dry weight was increased by Si treatment (Table 6), but there is no reflection in the photosynthesis. It is also contradictory that in the section 1, transpiration rate was decreased 30 % by Si treatment in the long term experiment, however, the same result could not be obtained in this experiment.

According to the results obtained in Chapter II, Si in dissolved or dispersed state is below 500 ppm  $\text{SiO}_2$  in rice plant. Under the pH of rice cell sap (generally 4 to 7), Si may be present in the form of monosilicic acid, and/or low molecular silicic acid. This form may not have possibility to take part in biochemical action. The results obtained in the section 1 revealed that rice plants can finish their life cycle even without Si. The result shown in Fig. 7 suggests that the fresh weight of -Si plants also increased with the progression of the growth, and Si effect showed an accumulative characteristics.

It must be noticeable that the measurement of photosynthesis by SPB-H2 was carried out on 3.4  $\text{cm}^2$  of leaf blade within 1 minute. If Si increases shoot dry weight 20 % after one month treatment, it will be understanding that the difference in photosynthesis between -Si plants and +Si plants can not be detectable within 1 minute using such an equipment as described above. This fact suggests that momentary measurement is not useful for Si studies.

To detect Si effect, longer period of treatment were made in Exp. 3, 4 and 5. Si effect appeared more when rice plants were treated with shading

(Table 8). This indirectly supports the "window theory". The experiments conducted under different humidities also suggest the possibility that Si may promote photosynthesis by reducing water stress. Ishihara and Saitoh (1987) studied the diurnal changes of photosynthesis in the single-leaf of the rice plants grown in the paddy field under submerged condition. They found that the leaf photosynthetic rate decreased to some extent in the midday on fine days. The dominant factor responsible for the decrease was attributed to decreasing  $\text{CO}_2$  supply through stomata to the mesophyll due to water stress (Hirasawa *et al.* 1989). Rice plant has a thin cuticle, and the cuticular transpiration is more than other plants though cuticular transpiration is much less compared to stomatal transpiration. As obtained in the section 1, the transpiration was decreased 30 % by +Si during whole growth period. This may contribute to promoting photosynthesis accumulatively by reducing water stress.

The results shown in Table 10 suggest another possibility of Si promoting photosynthesis of rice plants. This is that Si may improve light-receiving plant form. Although this effect was emphasized in fields with mutual shading in the community (Takahashi 1987), it is often ignored when rice plants are precisely cultured in green house in which there is not mutual shading. As well known, however, rice blades with Si have an erect form because of silicified cells, while those without Si have a droopy form. Erect leaves may utilize light more efficiently than droopy leave.

Above results reveal that Si may promote photosynthesis by improving light transmission, decreasing transpiration and improving light-receiving plant

form. All or either of three mechanisms are possible, depending on growth conditions such as humidity, temperature, light intensity, *etc.* So it is not surprising that sometimes Si effect appears easier, and sometimes hardly appear.

### Section 3 Possible mechanism of silicon effects on yield components

As obtained in the section 1, the filled spikelet percentage was most affected by Si among yield components. This result is in agreement with those reported by Mitsui and Takato (1960), Okuda and Takahashi (1961b), and Yoshida (1965).

Filled spikelet percentage is determined by many factors. Seo and Ota (1981, 1982a,b, c) reported that the hull plays an important role in filling spikelets. For normal development of spikelets, a high moisture condition within hull is necessary during ripening. Thus the capacity of hull keeping moisture is related to fertility or sterility of spikelets. As shown in Table 4, the hull also has a high content of Si as leaf blade, the transpiration of the hull may also be decreased by Si. In this section, effect of Si on the water retention capacity of the hull was studied.

## MATERIALS AND METHODS

Rice plants were cultured in the same method as described in the section 1. Spikelet samples were taken on the day of 10 (milky stage) and 40 (maturity stage) after heading. The water loss rate of the spikelets was measured immediately under the conditions of 30°C, 30% RH at the time indicated in figures. Water retention capacity was calculated from the water loss of spikelets during one hour, indicated by the rate of water content after one hour to total water content.

## RESULTS AND DISCUSSION

With no Si, the percentage of filled spikelets decreased nearly half of that with Si as shown in Fig. 5 in the section 1. The Si content of the hull reached as high as 15 % SiO<sub>2</sub> (Table 4). The water loss rate of the -Si spikelets was about 20 % more than +Si spikelets at both stages (Fig.11). The water loss was more at milky stage than at maturity stage. The water retention capacity during one hour increased 20% at milky stage and 10 % at maturity stage, respectively, with Si treatment.

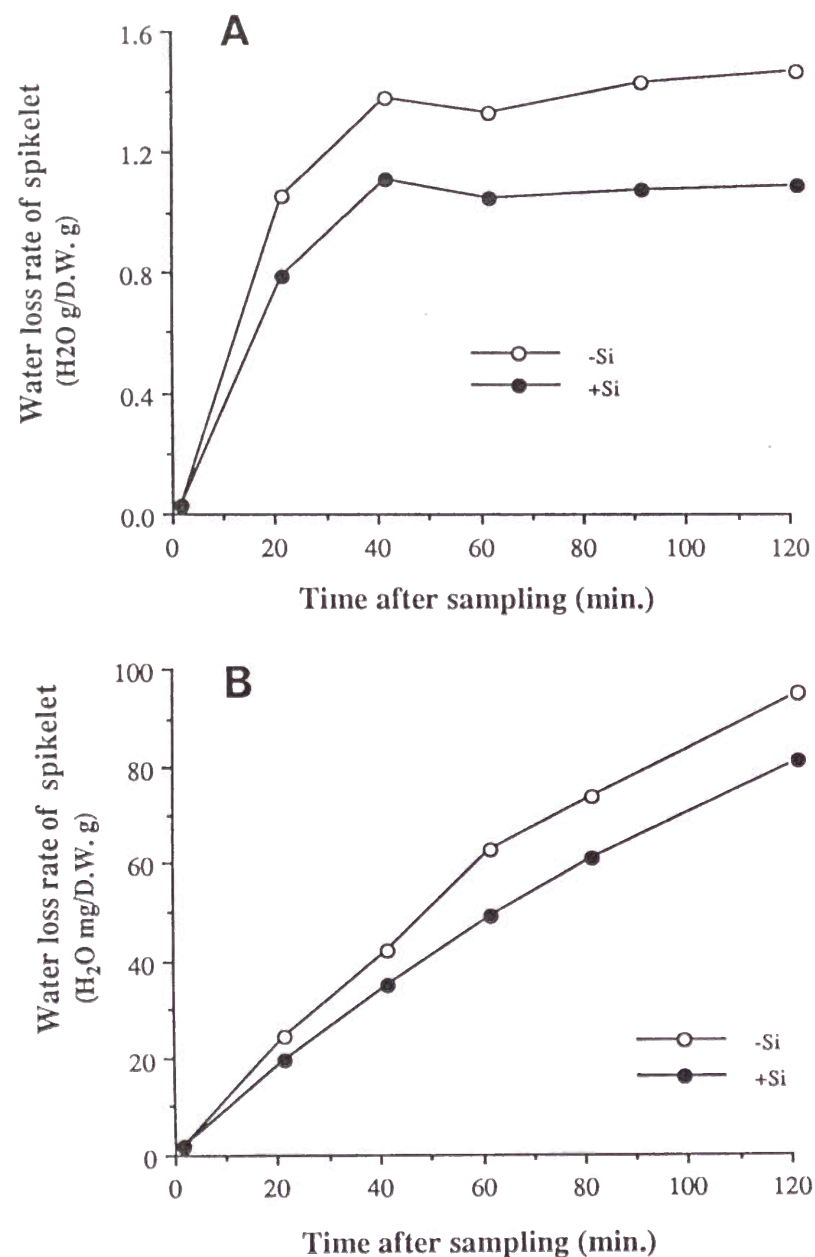


Fig. 8 The rate of water loss in spikelets treated with and without Si, sampled on the day of 10 (A) and 40 (B) after heading.

The length and width of hull has been determined before heading (Matsushima 1957). So filled spikelets percentage is mainly determined by the ability of assimilation in leaves and stems, translocation of assimilate from leaves to spikelets and the condition of ripening. In the section 2, the effect of Si on photosynthesis has been discussed. Ota and Yamada (1962), and Takahashi, Arai *et al.* (1966) reported that Si promoted translocation of assimilate. Both of these are related to the assimilate supply to the sink (hull). However, the hull is not only as a sink, but also plays an important role in the ripening of rice plant, especially in keeping moisture within it as stated above.

Table 11 Water retention capacity (%/hour) of spikelets under -/+Si treatment

Treatment	Stage	
	Milky-ripe	Maturity
-Si	52.2	70.7
+Si	62.2	77.0
+Si/-Si	1.19	1.09

Because the hull has no stoma, the transpiration occurs only from cuticle. Silica also deposits in the hull between the epidermis cell wall and the cuticle, forming cuticular-silica double layer (Yoshida 1962c, Seo and Ota 1982b). In

this experiment, Si decreased the water loss of spikelets, especially at milky-ripen stage (Fig. 8). The formation of cuticular-silica double layer, therefore may contribute to reducing excess water loss from the hull. This results in keeping a high moisture condition within hull, enabling the spikelets to finish normal development.

#### CHAPTER IV EFFECT OF SILICON ON RICE PLANT AT DIFFERENT GROWTH STAGES

It is clear from above experiments that Si is necessary for healthy growth of rice plants. Although Si is abundant in soil, little is available for plants. It is estimated that one third of paddy soils in Japan is deficient in available silicate. Now, several hundred thousands ton of silicate fertilizers are applied to paddy soils every year for increased rice production.

The silicate fertilizers, which have been used until now, mainly are slags which are by-products of iron manufacture industry. Their main composition is calcium silicate. Because both their solubility and available content of Si are low, a lot of amounts have to be applied. Thus these fertilizers have been used only as a basal application. However, with the development of new Si fertilizers (high content of water soluble Si), additional application of Si fertilizer becomes possible and easy. Therefore it is important for economical and effective application of Si fertilizer to analyze the differences in the effect of Si on rice plant depending upon the growth stages. In this chapter, the growth period of the rice plant was subdivided into three stages. The effect of Si on the growth and the characteristics of the uptake and distribution of Si at different growth stages were studied by the addition and removal of Si, respectively.



MATERIALS and METHODS

The cultivar Akebono (*Oryza sativa L.*) was also used in this experiment. The growth period of the rice plant was divided into three stages: vegetative stage, reproductive stage and ripening stage. The vegetative stage refers to the period from transplanting to panicle initiation, the reproductive stage from panicle initiation to heading, and the ripening stage from heading to maturity.

The experiment was subdivided into Experiment I and Experiment II (Fig. 9). In Experiment I the effect of Si removal on rice plant growth at different growth stages was analyzed. In Treatment A the plants were cultured in a solution with Si throughout the growth period. In Treatment B, C or D, Si was removed during the vegetative stage, reproductive stage and ripening stage, respectively. On the other hand, in Experiment II the effect of Si addition at different growth stages was analyzed. In Treatment E the plants were cultured in a solution devoid of Si throughout the growth period. In Treatment F, G or H, Si was added during the vegetative stage, reproductive stage and ripening stage, respectively.

The composition of the nutrient solution was based on Kimura B solution. The concentration was modified with the progression of growth (Okuda and Takahashi, 1961a). The water used for the experiments was distilled with a copper still. The culture solution was renewed once a week, and the pH of the solution was adjusted to about 5.5 with 0.2 N KOH. For the Si addition treatments 100ppm SiO<sub>2</sub> as silicic acid was supplied.

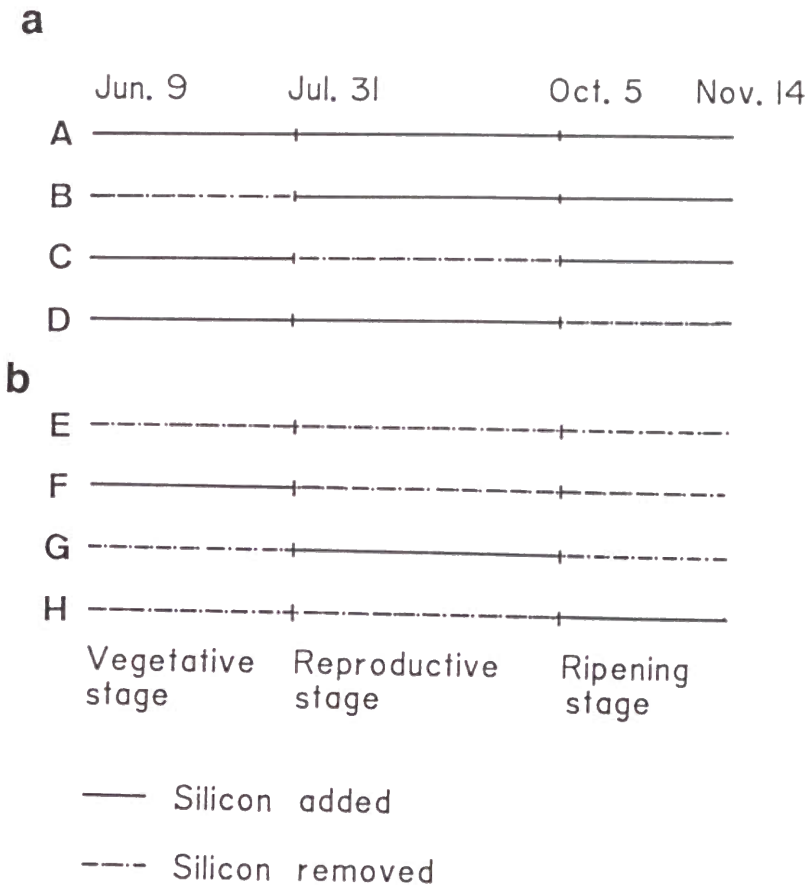


Fig. 9 Design of experiments. a and b represent Experiment I (Si removal experiment) and Experiment II (Si addition experiment), respectively.

The seeds of the rice plant were soaked in distilled water for one day, sown in a nursery bed in which acid washed polyethylene beads were used as rooting media. After 10 days, 1/4 strength Kimura B nutrient solution was supplied.

On Jun. 9, 1987, twenty-five days after sowing, selected seedlings were

transferred to culture pots lacking and containing Si, respectively (one seedling per pot) according to the experimental design (Fig. 9). Three replicates were made for each treatment. The experiment was carried out in a greenhouse from June to November, 1987.

On Jul. 31 (panicle initiation) and Oct. 5 (heading), the treatments were changed according to the experimental design (Fig. 9).

All the plants were harvested on Nov. 14 when the panicles were fully ripen. Each plant was separated into panicles, flag leaf, other leaf blades, stem (culm + leaf sheath) and roots. The dry weights, plant heights and yield components were determined. The Si contents were determined by the method described above.

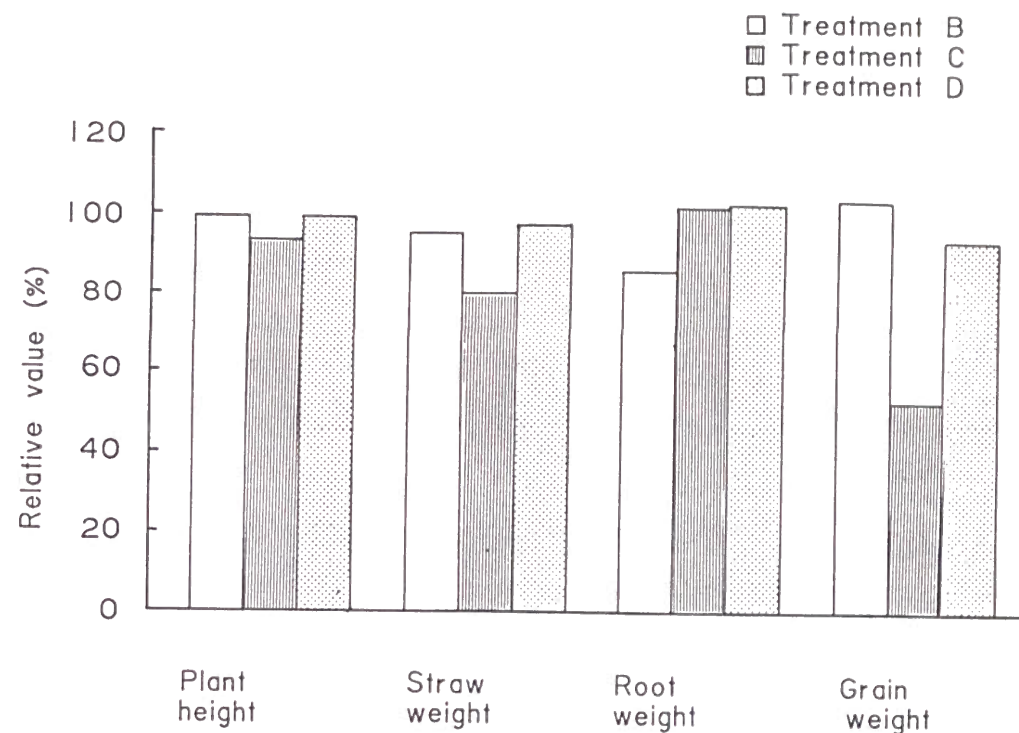
## RESULTS

### Exp.I Effect of the removal of Si at different growth stages

The values for plant height, dry weights of straw (stem+leaf blade) and grain per pot in Treatment C were remarkably lower than those in the other treatments (Fig. 10). The dry weights of straw and grain in Treatment C decreased by 20 and 50 percent, respectively, compared with those in Treatment A. The values of the corresponding parameters in the other treatments, however, were less influenced by the removal of Si.

Compared with Treatment A, the panicle number per plant in Treatment B and the spikelet number per panicle in Treatment C decreased by about 5 and 10

percent, respectively (Fig. 11). The percentage of filled spikelets in Treatment C decreased by about 40 percent, whereas that in Treatments B and D was less influenced. The 1,000-grain weight was hardly influenced by the removal of Si regardless of the growth stage.



*Fig. 10* Effect of the removal of Si at different growth stages on the growth of rice plants. Data are relative values of Treatment A (as 100).

Si uptake at different growth stages and the distribution in the respective plant parts were determined based on the difference in the uptake

between Treatment A and the other treatments (Tables 12 and 13). The uptake percentage of Si during the vegetative, reproductive and ripening stages was 10, 67 and 24, respectively. About 75 percent of Si in the leaf blades and 65 percent of Si in the stem were absorbed during the reproductive stage, whereas 76 percent of Si in the panicles was absorbed during the ripening stage.

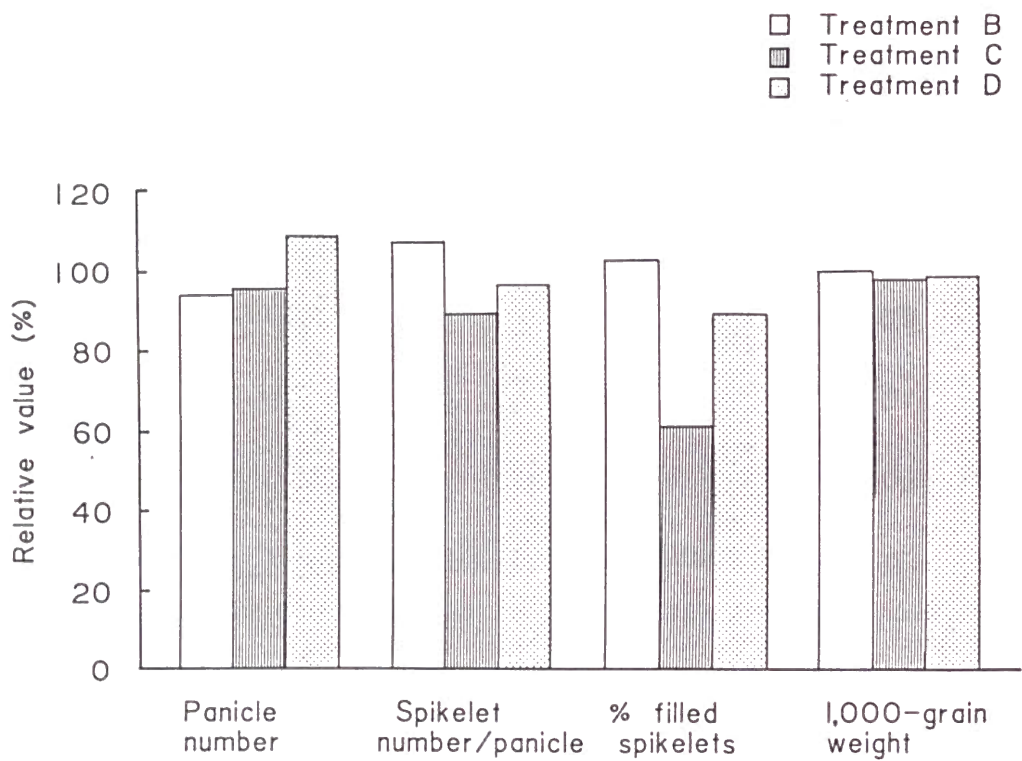


Fig. 11 Effect of the removal of Si at different growth stages on the yield components of rice plants. Data are relative values of Treatment A (as 100).

About 40 percent of the Si absorbed during the vegetative and

reproductive stages was present in the leaf blades (Table 13), while only 20 percent of the Si absorbed during the ripening stage was found in the leaf blades. More than 99 percent of the Si absorbed was present in the shoots.

Table 12 Uptake of silicon by rice plant during growth stages (Exp. I).

Plant part	Total silicon uptake (mg SiO <sub>2</sub> /pot)	Uptake percentage during <sup>a</sup>		
		Vegetative stage	Reproductive stage	Ripening stage
Panicle	920	0	24.0	76.0
Leaf blade	4,820	10.4	75.4	14.3
Stem	7,590	11.5	65.2	23.3
Shoot	13,300	9.6	66.5	23.8
Root	84	0	69.7	30.3
Total	13,400	9.6	66.5	23.8

<sup>a</sup> Uptake percentage, silicon uptake during each stage/total silicon uptake; Silicon uptake during each stage was calculated from the difference of uptake between Treatment A and the other treatments; Total silicon uptake is expressed by the sum of silicon uptake during each stage.



Table 13 Distribution of silicon in plant parts during stages (Exp. I)

Stage	Distribution percentage in				
	Panicle	Leaf blade	Stem	Shoot	Root
Vegetative	0	36.4	63.6	100	0
Reproductive	2.5	41.0	55.9	99.4	0.7
Ripening	22.0	21.6	55.6	99.2	0.8

The Si contents of all the plant parts in Treatments B and D were nearly the same as those of Treatment A except for the Si content of the panicle in Treatment D (Table 14), whereas those of Treatment C except for the panicle were considerably lower, especially for the flag leaf. The Si content of the flag leaf in Treatment C decreased to 5 percent, whereas that in the other treatments was hardly affected by the removal of Si.

Table 14 Silicon contents (% SiO<sub>2</sub>) in plant parts depending on the treatments (Exp. I)

Treatment	Stage at which silicon was removed	Panicle	Flag leaf	Leaf blade	Stem	Root
A	No removal	3.24	10.9	20.4	11.8	0.93
B	Vegetative	3.43	12.0	18.1	11.1	1.33
C	Reproductive	3.53	5.19	6.73	4.59	0.34
D	Ripening	0.77	9.42	17.2	9.30	0.66

## Exp.II Effect of the addition of Si at different growth stages

The effect of the addition of Si on the root dry weight was not clear (Fig. 12). The values for the plant height, dry weights of straw (leaf blade + stem) and grain in Treatment G were considerably larger than those of other treatments. The dry weights of grain and straw in Treatment G increased by 243 and 30 percent, respectively, over those of Treatment E. The corresponding values in Treatment F also increased by the addition of Si during the vegetative stage, but were lower than those of Treatment G, especially for the grain weight. The effect of the addition of Si during the ripening stage was negligible.

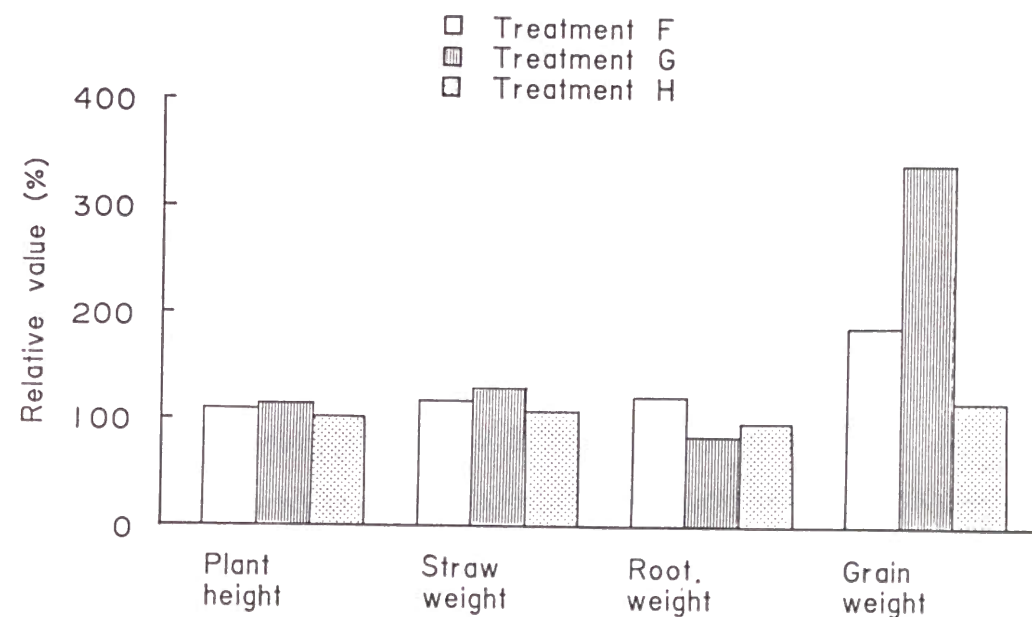


Fig. 12 Effect of the addition of Si at different growth stages on the growth of rice plants. Data are relative values of treatment E (as 100).



Compared with Treatment E, the percentage of filled spikelets in Treatment G increased by about 2.5 times (Fig. 13), while that of Treatment H was hardly affected. The spikelet number in Treatment G increased by 32 percent. The panicle number and 1,000-grain weight were not remarkably influenced by the removal of Si regardless of the growth stage.

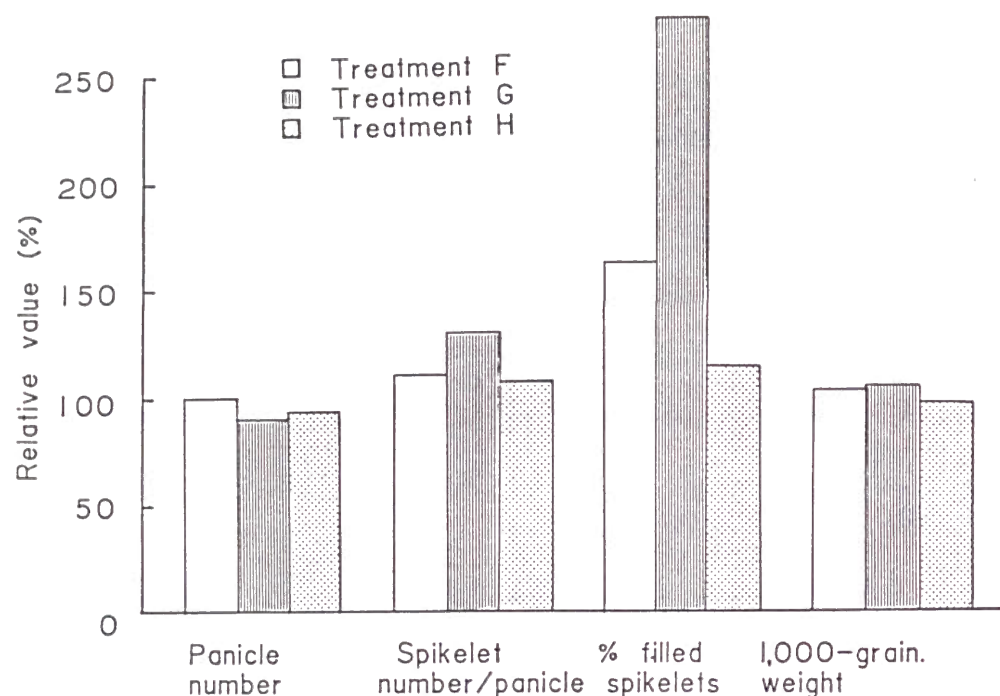


Fig. 13 Effect of the addition of Si at different growth stages on the yield components of rice plants. Data are relative values of Treatment E (as 100).

The uptake percentages of Si during the vegetative, reproductive and ripening stages were 9, 65 and 26, respectively (Table 15). Seventy percent of Si in the leaf blade and 66 percent of Si in the stem were absorbed during

the reproductive stage, whereas 75 percent of Si in the panicle was absorbed during the ripening stage. Nearly half of the Si absorbed during the vegetative and reproductive stages was present in the leaf blades (Table 16), whereas only 30 percent of the Si absorbed during the ripening stage was found in the leaf blade. More than 99 percent of the Si absorbed was found in the shoots regardless of the growth stage. The Si contents of the flag leaf, leaf blades and stem in Treatment G were much higher than those in other treatments (Table 17). The Si content of the flag leaf in Treatment G amounted to 10 percent, while that in Treatments F and H was only 0.2 and 5.2 percent, respectively.

Table 15 Uptake of silicon by rice plant during growth stages (Exp. II).

Plant part	Total silicon uptake (mg SiO <sub>2</sub> /pot)	Uptake percentage during <sup>a</sup>		
		Vegetative stage	Reproductive stage	Ripening stage
Panicle	770	1.7	23.5	74.8
Leaf blade	5,930	12.3	70.2	17.6
Stem	6,840	7.3	65.9	26.8
Shoot	13,600	9.2	65.4	25.5
Root	76	6.5	47.4	46.1
Total	13,700	9.1	65.3	25.6

<sup>a</sup> Uptake percentage, silicon uptake during each stage/total silicon uptake; Silicon uptake during each stage refers to the uptake in Treatment F, G, and H. Total silicon uptake is expressed by the sum of silicon uptake during each stage.

Table 16 Distribution of silicon in plant parts during stages (Exp. II)

Stage	Distribution percentage in				
	Panicle	Leaf blade	Stem	Shoot	Root
Vegetative	1.1	58.4	40.1	99.6	0.4
Reproductive	2.0	46.8	50.8	99.6	0.4
Ripening	16.6	29.9	52.5	99.0	1.0

Table 17 Silicon contents (% SiO<sub>2</sub>) in plant parts depending on the treatments (Exp. II)

Treatment	Stage at which silicon was added	Panicle	Flag leaf	Leaf blade	Stem	Root
E	No addition	0.02	0.05	0.20	0.11	0.04
F	Vegetative	0.07	0.20	3.43	1.00	0.04
G	Reproductive	0.77	9.99	17.6	8.20	0.45
H	Ripening	3.11	5.20	4.86	4.06	0.39

## DISCUSSION

The effect of Si on the growth of the rice plant was studied from both aspects: the removal and the addition of Si at different growth stages. Both the

removal and addition experiments showed that the plant height, the dry weights of straw and grain markedly increased or decreased by the addition or removal of Si during the reproductive stage (Figs. 10 and 12). The effect of either the addition or the removal of Si during the vegetative and ripening stages was small.

The reproductive stage which refers to the period from panicle initiation to heading is characterized by culm elongation, decrease in the tiller number, emergence of the flag leaf, booting, heading and flowering. As a result this stage is most important for the determination of the panicle number, spikelet number and the fertility of panicles. In the current studies, both the Si removal and addition experiments showed consistently that during this stage, about 66 percent of Si in the whole plant was absorbed (Tables 12 and 15), and was mainly translocated into the leaf blades (41 to 47 percent) (Tables 13 and 16). By the removal of Si during the reproductive stage, the Si content of the flag leaf decreased to half of that in Treatment A which was cultured in the solution with Si throughout the growth period (Table 14). Conversely, by the addition of Si only at this stage, the Si content of the flag leaf was as high as that of Treatment A (Table 17).

As discussed in the Chapter III, Si in the leaf blades are the most important for promoting photosynthesis and translocation of assimilate to the panicle. Due to Si supply during the reproductive stage, a high content of Si in leaf blades, especially in the flag leaf which contributes significantly to the yield was obtained. This may contribute to the increase not only in dry matter production,

but also in grain weight.

About 25 percent of Si in the whole rice plant was absorbed during the ripening stage (Tables 12 and 15), however, in contrast to the Si absorbed during the reproductive stage, a smaller amount of Si was introduced into the photosynthetic organ--leaf blades (Tables 13 and 16), especially into the flag leaf (Tables 14 and 17). Therefore, although about 75% of Si in the panicle was absorbed during the ripening stage (Tables 12 and 15), the percentage of filled spikelets was still low if Si was only added during this stage. This may be because there was no sufficient source activity to support the growth of all the spikelets.

During the vegetative stage, only 10 percent of Si in the whole rice plant was absorbed (Tables 12 and 15), and as Si in plant is immobile (Yoshida, 1962d), the Si absorbed during this stage could not affect the growth in the later period.

Based on these results, it can be concluded that the supply of Si during the reproductive stage is most important for rice growth.

## CHAPTER V INTERACTION BETWEEN SILICON AND PHOSPHORUS IN RICE PLANTS AND SOIL

Many researchers have reported a beneficial effect of Si on plant growth when available P is low (Brenchley *et al.* 1926, Gile and Smith 1925, Hall and Morison 1906, Lemmermann and Wiessmann 1922, Syouji 1981, Toth 1939). Explanations for this effect, however, are various and even contradictory. Different experimental materials and methods may be an important reason for the different results. In this chapter, the interaction between Si and P in rice plant and in soil was studied using water culture and soil culture, respectively.

### Section 1 Effect of Si on the growth and P uptake of rice plants at different P levels

The beneficial effect of Si when available P is low, has been explained as a partial substitution of Si for P (Hall and Morison, 1906) or an improvement of P availability in soil (Noda and Komai 1958, Roy *et al.* 1971, Smyth and Sanchez 1980, Syouji 1981). Although the partial substitution of Si for P in physiological processes is doubtful, an interaction between Si and P in plants may occur.

Si has also been found to have a beneficial effect on the growth of rice plants, when the P level in solution was high (Tanaka and Takahashi 1980).



Recently, Ma and Takahashi (1989) found that P uptake markedly decreased and plant growth was promoted when Si was added to a culture solution containing high P, however the reasons for this were not explained.

In this section, the effect of Si on P uptake, as well as the effect of Si on rice growth under different P levels in solution are discussed with a pot experiment.

## MATERIALS AND METHODS

Rice seedlings were prepared by the same method described before. Three seedling each of 30 days age were transplanted into 3 liter pots with modified full strength Kimura B solution: KCl substituted for  $\text{KH}_2\text{PO}_4$ . The pots were arranged on green house tables in a completely randomized design with +/- Si main treatments and 1, 15, 50 ppm  $\text{P}_2\text{O}_5$  as sub treatments in 3 replicates. -Si treatments contained no Si and +Si treatments contained 100 ppm  $\text{SiO}_2$  as silicic acid. P sub treatments were supplied as  $\text{NaH}_2\text{PO}_4$ . The 1 ppm  $\text{P}_2\text{O}_5$  was considered low, 15 ppm was medium since it was approximately the same as full strength Kimura B solution, and 50 ppm was considered high. Other nutrients concentrations were the same as full strength Kimura B solution. The solution was adjusted to about pH 5.5 with 0.2 N KOH and was renewed each week. One month after transplanting, the rice plants were harvested, shoots and roots separated, and shoots immediately freeze-dried. Organic P and inorganic P were separated by trichloroacetic acid (TCA) as

shown in Fig. 14 (Committee on the Methods of Crop Analysis 1982). The P content was determined by ammonium metavanadate colorimetric method after Kjeldahl digestion, the content of Fe and Mn by the atomic absorption spectrochemical method after nitric acid digestion. The method for Si analysis was the same as described before.

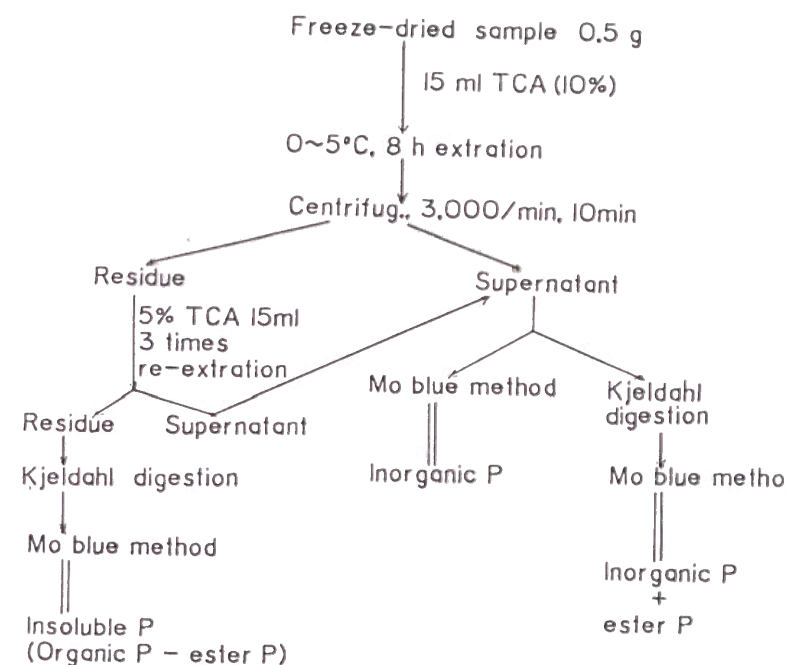


Fig. 14 Separation method for phosphorus fraction.

## RESULTS

Shoot dry weight in +Si increased with increasing P, while those in -Si reached a maximum when P was 15 ppm  $\text{P}_2\text{O}_5$  (Fig. 15). Dry weight of shoots grown in 1, 15, 50 ppm  $\text{P}_2\text{O}_5$ , increased 40, 32 and 61 %, respectively

with +Si, compared to -Si.

The percent of inorganic P in the shoots increased significantly with increasing P, but the increase in -Si was more than double compared to +Si, except at 1 ppm  $P_2O_5$  (Fig. 16). Inorganic P in shoots grown in 50 ppm  $P_2O_5$  and -Si reached 1.4 %; much higher than the 0.55 % in shoots grown with +Si. Organic P was not strongly affected by changes in the Si or P of the nutrient solution. However, total P (inorganic + organic) of shoots in 50 ppm  $P_2O_5$  and +Si was 0.71 % of dry weight; lower than the 0.90% in shoots grown in only 15 ppm  $P_2O_5$  and -Si.

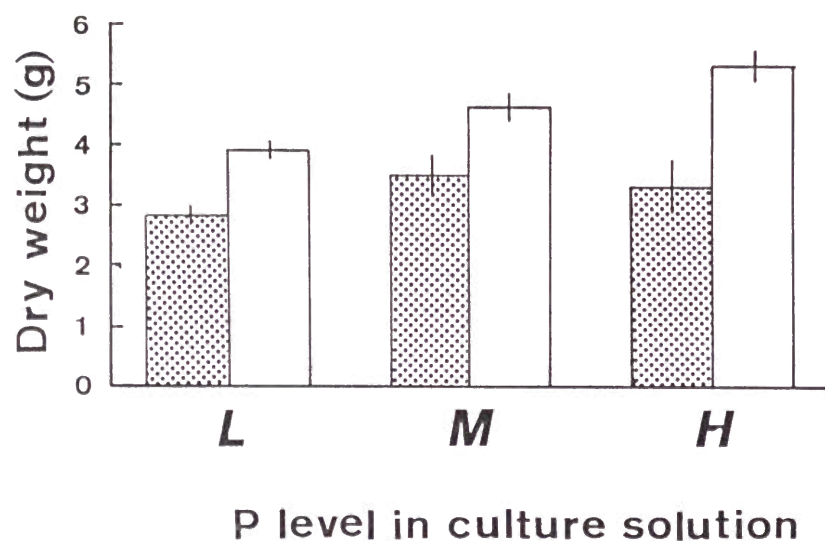


Fig. 15 Dry weight of shoots grown on a nutrient solution with (□) or without (▨) Si and with one of three P levels. L, M and H represent low (1 ppm  $P_2O_5$ ), medium (15 ppm) and high (50 ppm) P levels, respectively. Vertical lines on bars represents SD.

In -Si, the total weight of P taken up by rice plants was greater at all P levels, compared to +Si, except at 1 ppm  $P_2O_5$  (Fig. 17). Total P uptake in the 15 and 50 ppm  $P_2O_5$  media was 27 and 30 % less in +Si, respectively. The effect of Si and increasing P on the amount of organic and inorganic P showed the same trends as in Fig. 16.

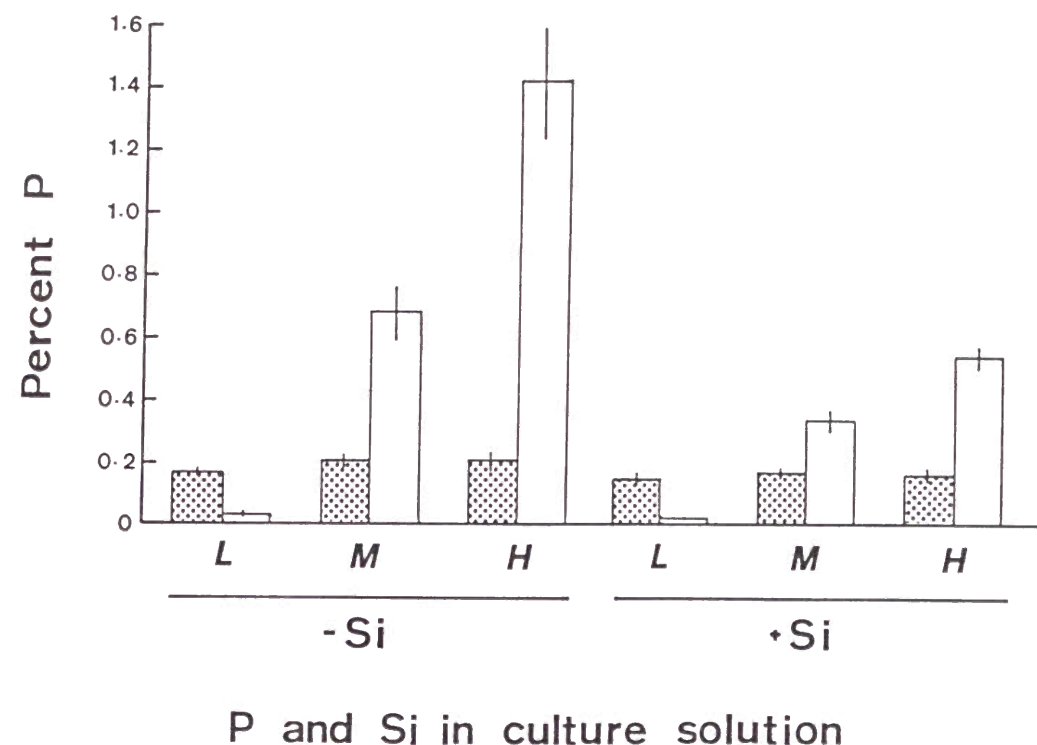


Fig. 16 Percent organic P (▨) and inorganic P (□) of shoots (% dry wt.) grown on a nutrient solution with and without Si and with one of three P levels. L, M and H represent Low (1 ppm  $P_2O_5$ ), Medium (15 ppm) and High (50 ppm) P levels, respectively. Vertical lines on bars represent SD.

The Si concentration in rice shoots decreased slightly with increasing P levels (Table 18). However, Si uptake by rice plant was not significantly affected. The concentration of Fe and especially Mn in rice shoots was decreased by +Si at all P levels (Table 19). The uptake of Fe and Mn was decreased by an average of about 20 and 50 %, respectively. The P/Fe ratio within the shoots only increased in +Si at the 1 ppm P<sub>2</sub>O<sub>5</sub> level compared to -Si, while the P/Mn ratio increased at all levels with +Si, especially at 1 ppm P<sub>2</sub>O<sub>5</sub> (Table 20).

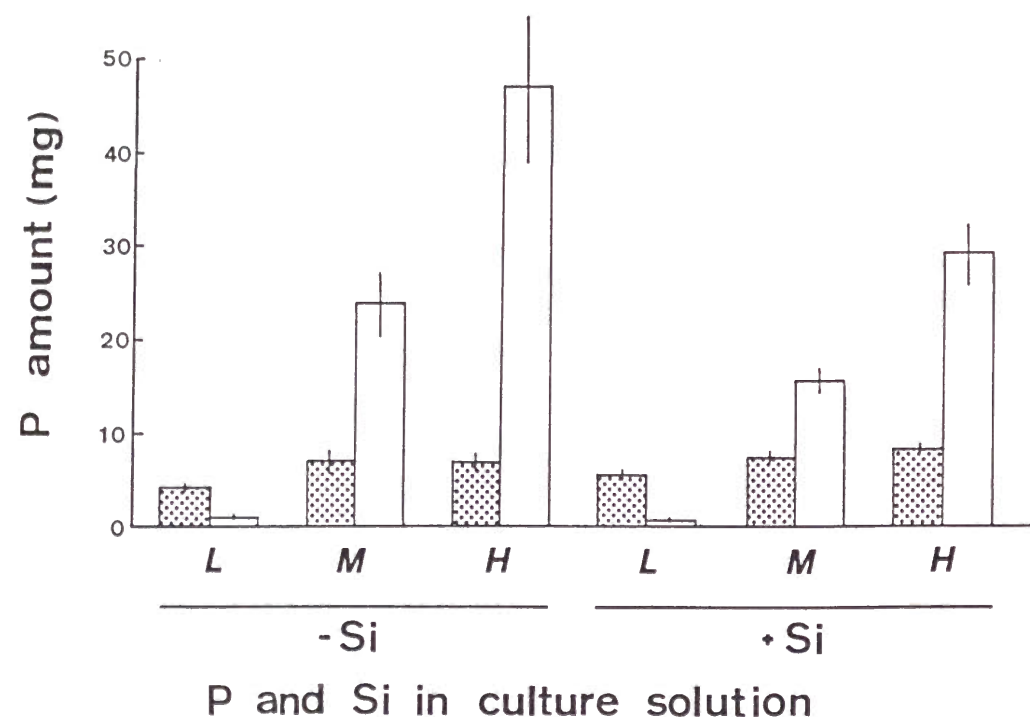


Fig. 17 Total organic P (▨) and inorganic P (□) of shoots (mg) grown on a nutrient solution with and without Si and with one of three P levels. L, M and H represent Low (1 ppm P<sub>2</sub>O<sub>5</sub>), Medium (15 ppm) and High (50 ppm) P levels, respectively. Vertical lines on bars represent SD.

Table 18 The concentration and uptake of Si in rice shoots grown on nutrient solution with one of three P levels. Values are means (n=3) with SD within parentheses.

P level (P <sub>2</sub> O <sub>5</sub> ppm)	Si (% dry weight)	Si uptake (mg)
1	4.98 (0.29)	194.7 (5.2)
15	4.74 (0.19)	216.4 (3.8)
50	3.95 (0.44)	210.2 (15.3)

Table 19 The concentration and uptake of Fe and Mn in rice shoots grown on nutrient solutions with or without Si and with one of three P levels. Values are means (n=3) with SD within parentheses.

P level (P <sub>2</sub> O <sub>5</sub> ppm)	Concentration(ppm)				Uptake (mg)			
	Fe		Mn		Fe		Mn	
	+Si	-Si	+Si	-Si	+Si	-Si	+Si	-Si
1	98	166	194	615	0.39	0.40	0.76	1.73
	(5)	(17)	(23)	(16)	(0.02)	(0.05)	(0.09)	(0.09)
15	94	151	257	708	0.40	0.53	1.21	2.45
	(17)	(37)	(5)	(67)	(0.06)	(0.15)	(0.03)	(0.07)
50	88	143	246	705	0.47	0.48	1.31	2.31
	(10)	(21)	(8)	(77)	(0.07)	(0.14)	(0.05)	(0.19)

Table 20 The P/Fe and P/Mn ratios in rice shoots grown on nutrient solutions with or without Si and with one of three P levels. Values are means (n=3) with SD within parentheses.

P level (P <sub>2</sub> O <sub>5</sub> ppm)	P/Fe		P/Mn	
	-Si	+Si	-Si	+Si
1	12 (1)	17 (1)	3 (1)	9 (1)
15	59 (7)	57 (5)	13 (2)	19 (2)
50	113 (20)	80 (8)	23 (2)	29 (2)

## DISCUSSION

In this study, the dry weight of shoots increased with +Si at all P levels (Fig. 15), although dry weight increased relatively more when P was low (1 ppm P<sub>2</sub>O<sub>5</sub>) or high (50 ppm), compared to the medium level (15 ppm). When P was low in solution, the dry weight increase in +Si was not accompanied by an increase in total shoot P (Figs. 16 and 17), suggesting that the increase (Fig. 15) was not caused by the promoting of P uptake.

Roy *et al.* (1971) found that silicate application tended to increase the P concentration in the green tops of sugarcane (metabolically more active tissue) and decrease P in the stalk (metabolically less active tissue) when P nutrition was low. This tendency did not occur when P nutrition was high. These

observations suggest that P utilization in the plant may be improved by +Si when available P is low. Certain facts suggest that P availability may be controlled by the levels of Mn and Fe in plants when P is low. P is translocated and redistributed in plants as inorganic P, and since a strong affinity exists between P and Fe or Mn, the relationship of these elements may affect P nutrition. Biddulph (1953) found that P precipitated with Fe in plants, and Bortner (1935) reported that P might combine with Mn into an inactive form. Thus, plant P/Fe and P/Mn ratios may be more indicative of P nutrient than P concentration.

Okuda and Takahashi (1962c) reported that Si promoted the oxidation power of roots and thus decreased the solubility and uptake of Fe and Mn. In this experiment, shoot Fe and Mn uptake were decreased by +Si (Table 19), although P concentration did not change between -Si and +Si when P was low (Fig. 16). Thus P/Fe and P/Mn ratios were increased by +Si (Table 20), suggesting that +Si increased P availability in the shoots.

Inorganic P concentration in plants depends on the level of P and Si in the nutrient solution (Figs. 16 and 17). Compared to inorganic P, organic P is much less dependent on levels in the nutrient solution. Inorganic P within plant is necessary for metabolism and storage, but high concentrations inhibit enzyme reactions, create abnormal osmotic pressure in the cell, *etc.* (Yoneyama 1988). Thus part of the dry weight reduction of shoots grown in 50 ppm P<sub>2</sub>O<sub>5</sub> and -Si may have resulted from high inorganic P within the plants. In other words, +Si is beneficial to the plant when P availability is high, by



reducing P uptake and thereby reducing inorganic P within the plant. This statement suggests that +Si broadens the range of optimal P in the medium and is expected to be useful in circumstances where excessive P fertilizer has been applied.

The decrease in P uptake by +Si may be related to the Si in the roots (Ma and Takahashi 1989). Si deposits in the apoplastic space of roots (Parry and Soni 1972), this may affect apoplastic flow and permeability of P when P is high in the solution.

Although the concentration of Si in shoots slightly decreased with increasing P in solution (Table 18), total uptake of Si was not significantly affected, suggesting that the reduced Si concentration resulted from dilution via Si promoted growth (Fig. 15). Thus, while P uptake was strongly influenced by Si, the reverse was not true.

From the above results, +Si had a beneficial but indirect effect on plant growth when P was low or high in the nutrient solution. The mode of action for this indirect effect differed according to the P level in solution. When P was low, +Si caused a decrease in Fe and Mn uptake and thus promoted P availability within plant. When P was high, +Si reduced P uptake and thus inorganic P concentration in shoots.

## Section 2 Effect of silicic acid on rice plants in a P-deficient soil

Fisher (1929) indicated that an increase in barley yield after the application of

sodium silicates, resulted from increased P availability in the soil. Bastisse (1947) reported that adsorbed P could be displaced by Si. The displacement of P from certain soils by Si was also demonstrated by adsorption isotherms (Laws 1951, Obihara and Russell 1972). Silva (1971) reviewed most of the work conducted in Hawaii and also concluded that Si may replace P at adsorption sites.

Roy *et al.* (1971) reported that silicate applications decreased P adsorption in certain acid soils. Syouji (1981) studied the utilization of adsorbed P by crops from the viewpoint of energy and resource conservation. He found little conversion of P from slightly soluble to soluble forms after the application of calcium silicate, but P adsorption was prevented. Kundu *et al.* (1988) confirmed these results and reported the time-dependent nature of Si in reducing P adsorption.

The above reports indicate that an increase in soil P availability is attributable to a Si effect. It should be noted, however, that in all abovementioned experiments either sodium or calcium silicate was used as the Si source, or P adsorption and desorption occurred in highly alkaline solutions where pH was above 8. The influence of pH on P availability was ignored in the reports. Furthermore, except in alkaline soils, Si generally exists as monosilicic acid in soil solutions and is adsorbed as  $\text{Si(OH)}_4$  (McKeague and Cline, 1963a and b). It is not known whether the behavior of Si in soil is dependent on its applied form, silicic acid or silicate. In this section, the effects of silicic acid on the growth of rice and on P availability in a P-deficient



soil are discussed.

MATERIALS AND METHODS

The soil used in the experiment, taken from Yakuno-cho, Kyoto Metropolitan Prefecture of Japan, is a light clay (Table 21). The soil was characterized by low available phosphate and high phosphate absorption coefficient. The soil was derived from sediments of weathered basalt, but the upper part of the profile received an addition of volcanic ash (Miura, 1986).

Table 21 Some properties of Yakuno soil <sup>a</sup>

Soil texture	pH	CEC	C(%)	N(%)	PAC	AVP	AVSi
LC	4.5	22.7	9.02	0.33	2242	5.98	25.89

<sup>a</sup>CEC: meq/100 g soil  
PAC: Phosphate adsorption coefficient, P<sub>2</sub>O<sub>5</sub> mg/100 g soil  
AVP: Available phosphate, P<sub>2</sub>O<sub>5</sub> mg/100 g soil  
AVSi: Available silicate, SiO<sub>2</sub> mg/100 g soil

Rice experiment

A completely randomized design with 4 replications was prepared using a combination of silicic acid and moisture treatments. Fractions of soil

that had passed a 2-mm sieve were used for pot culture of rice (*Oryza sativa* L. cv. Akebono). The soil had previously received 0 or 0.47 mg Si g<sup>-1</sup> soil (1 mg as SiO<sub>2</sub>) (-Si and +Si, respectively) as silicic acid. Rice seeds were soaked in distilled water for one day and then sown 30 per pot in pots each containing 300 g of treated soil. Pot soil was kept in a water-saturated state until seedling establishment. Seedlings were then thinned to 25 per pot and the soil was irrigated with distilled water to create two moisture conditions; flooded and nonflooded. For the nonflooded condition, pot soil was maintained at field capacity with supplied water daily. The flooded condition was maintained at a standing depth of 2 cm. No fertilizer was applied. Plants were grown for one month after sowing in a greenhouse and then harvested for analysis. The concentrations of P, Si, Fe and Mn in shoots were analyzed by methods described above.

Adsorption experiment

Three replicates each of two gram samples of soil, previously received 0, 0.23, 0.47, or 0.94 mg Si g<sup>-1</sup> soil as silicic acid, were equilibrated in 40-ml plastic centrifuge tubes for 5 days at 20°C with 30 ml of 0.01M CaCl<sub>2</sub> containing 12 mM P as Ca(H<sub>2</sub>PO<sub>4</sub>)<sub>2</sub>H<sub>2</sub>O. Two drops of toluene per tube were added. Tubes were shaken twice daily. After 5 days samples were centrifuged, filtered and analyzed for P in the supernatant using the molybdenum blue colorimetric method. Phosphorus which had disappeared from the solution was considered to have been adsorbed.

### Desorption experiment

For P desorption experiment, three replicates each of ten gram samples of soil, previously received 0 or 4 mg P g<sup>-1</sup> soil as Ca(H<sub>2</sub>PO<sub>4</sub>)<sub>2</sub>.H<sub>2</sub>O, were equilibrated for 5 days at 20°C with 25 ml of 0.01M CaCl<sub>2</sub> containing a range of Si concentrations as indicated in the figures as silicic acid. P in the supernatant was determined using the procedures described above, and Si using the colorimetric molybdenum blue method. P which appeared in the solution or Si which disappeared from the solution were considered to have been desorbed or adsorbed, respectively.

For Si desorption experiment, three replicates each of ten gram samples of soil, previously received 0 or 0.47 mg Si g<sup>-1</sup> soil, were equilibrated with 25 ml of 0.01M CaCl<sub>2</sub> containing a range of P concentrations as indicated in figure as Ca(H<sub>2</sub>PO<sub>4</sub>)<sub>2</sub>.H<sub>2</sub>O under conditions described above. After equilibration, Si in the supernatant was determined as above. Si which increased in the solution was considered to have been desorbed.

## RESULTS

Shoot dry weight increased significantly with +Si under both flooded and nonflooded conditions (Table 22). The P concentration of shoots with +Si did not increase compared to -Si under either nonflooded or flooded condition. Under +Si, shoot Si concentration was increased, Mn significantly decreased, and Fe was relatively unchanged. Because of decreased Mn, the P/Mn ratio

within shoots increased 12 percent under nonflooded condition and 32 percent under flooded condition, compared to -Si. The shoot P/Fe ratio was not increased by +Si in this experiment.

*Table 22* Dry weight and elemental concentrations in shoots under different moisture conditions and silicic acid treatments

Treatment	Nonflooded		Flooded		LSD (0.01)
	-Si	+Si <sup>a</sup>	-Si	+Si	
Dry weight (g)	1.34	1.52	1.40	1.61	0.10
Si (%)	1.44	2.81	2.10	3.58	0.17
P (ppm)	974	880	1041	1030	89.6
Fe (ppm)	96.1	84.6	126	116	21.1
Mn (ppm)	1870	1518	3696	2761	265
P/Fe	10.1	10.4	8.3	8.9	
P/Mn	0.52	0.58	0.28	0.37	

<sup>a</sup> Silicic acid was added at 0.47 mg Si g<sup>-1</sup> soil. Soil pH with +Si was the same as -Si.

In the adsorption and desorption experiments, P adsorption was about 175  $\mu$ mol g<sup>-1</sup> soil by samples which had received a range of silicic acid from 0 to 0.94 mg Si g<sup>-1</sup> soil (Table 23). P adsorption was not decreased by a previous addition of silicic acid. A range of silicic acid concentration did not

cause P desorption in soil samples which had received either 0 or 4 mg P g<sup>-1</sup> soil (Fig. 18).

Table 23 Effect of a previous application of silicic acid on P adsorption

Treatment <sup>a</sup>	P adsorbed ( $\mu\text{mol g}^{-1}$ soil)
Si0	175.2
Si1	173.9
Si2	175.2
Si3	175.5

<sup>a</sup> Si0, Si1, Si2 and Si3 represent soil samples which had previously received 0, 0.23, 0.47, or 0.94 mg Si g<sup>-1</sup> soil as silicic acid.

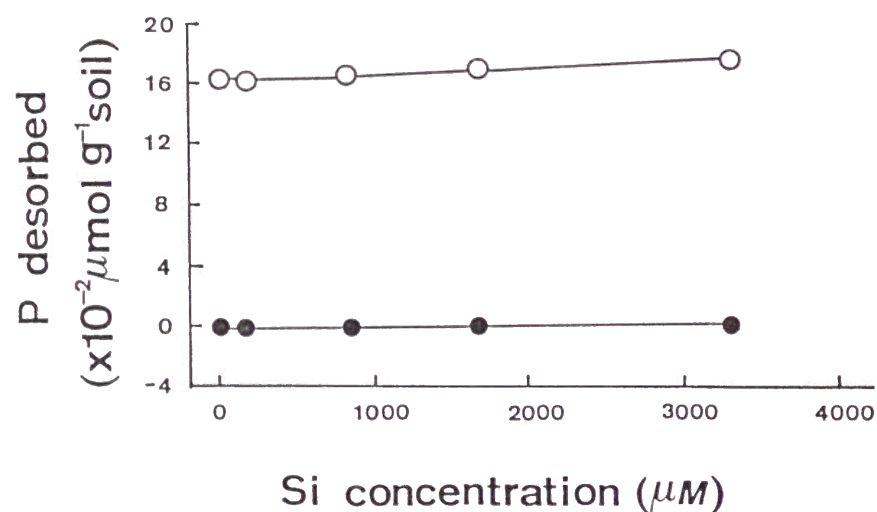


Fig. 18 Effect of Si concentration on P displacement in soil samples which had previous received 0 (●) or 4 mg P g<sup>-1</sup> soil (○).

Si adsorption responded linearly to Si concentrations, but was significantly reduced in soil samples which had previously received P (Fig. 19). Si adsorption ranged from -32 to +567x10<sup>-2</sup>  $\mu\text{mol g}^{-1}$  soil in samples which had received no P, and from -153 to +216x10<sup>-2</sup>  $\mu\text{mol g}^{-1}$  soil in samples which had previously received P. Si desorbed by P ranged from 34 to 44 x10<sup>-2</sup>  $\mu\text{mol g}^{-1}$  soil in samples which had received no Si, and from 82 to 104x10<sup>-2</sup>  $\mu\text{mol g}^{-1}$  soil in samples which had received Si (Fig. 20). Si desorption increased with increasing P concentration in the solution.

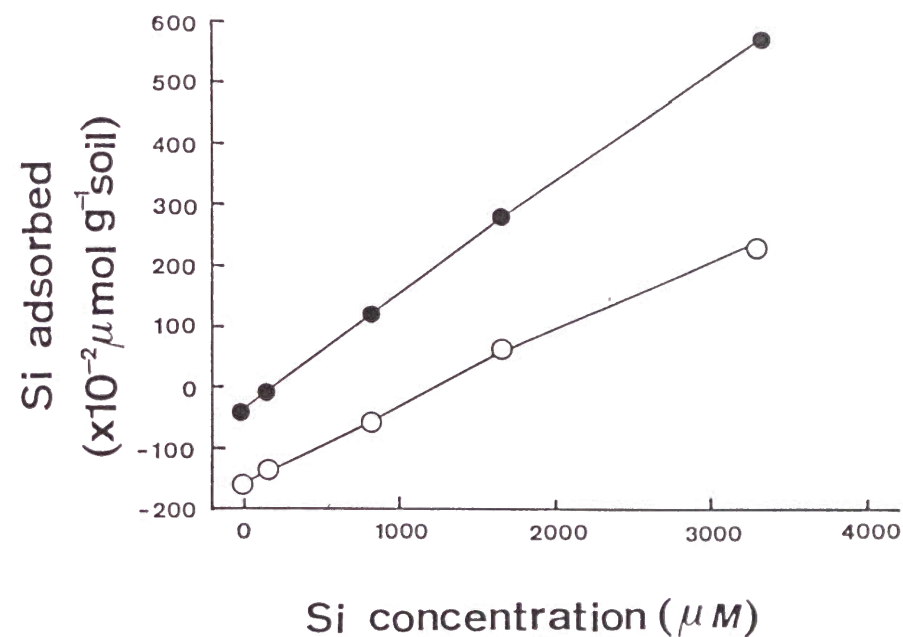


Fig. 19 Si adsorption by soil samples which had previously received 0 (●) or 4 mg P g<sup>-1</sup> soil (○).



## DISCUSSION

Silicic acid was used as the Si source, rather than a silicate salt, to separate the pH effect caused by silicate application from the Si effect. Shoot dry weight significantly increased with +Si, but was not accompanied by increased P concentration in shoots. Likewise in the adsorption and desorption experiments, P adsorption was not decreased by a previous addition of silicic acid (Table 23) nor was P desorption affected by a range of silicic acid concentrations (Fig. 18). These observations suggest that silicic acid did not affect P availability in Yakuno soil.

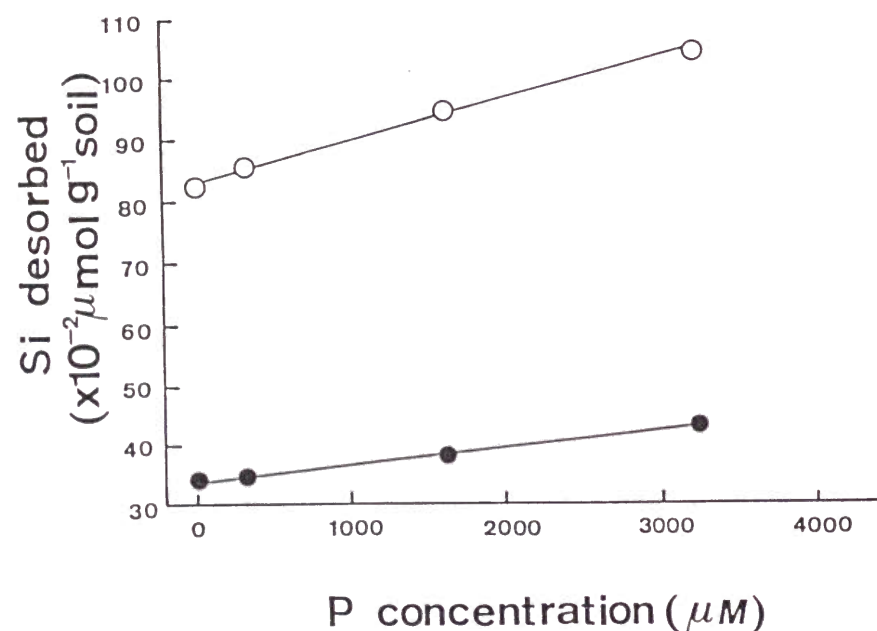


Fig. 20 Effect of P concentration on Si displacement in soil samples which had previously received 0 (●) or 0.47 mg Si g<sup>-1</sup> soil (○).

Both P and Si were adsorbed by the soil (Table 23, Fig. 19). However, much more P was adsorbed than Si although the soil/solution ratios employed were some different. Miura (1986) indicated that Yakuno soil was rich in Al-humus complexes. Wada and Gunjigake (1979), and Shoji and Fujiwara (1984) found that Al-humus complexes have a great affinity for P, and that P adsorption by nonallophanic soils is mainly governed by Al-humus complexes. In addition, Saito and Shoji (1984) reported that Al in Al-humus complexes has a low reactivity with Si. These observations suggest that Yakuno soil has a much higher affinity for P than for Si.

Results shown in Figs. 19 and 20, indicate that some sites of Si adsorption may be the same as those of P. Thus added P may not only decrease Si adsorption, but may also displace adsorbed Si because of its higher affinity to the site, however the reverse is not true.

The decrease in P adsorption by Si reported by Noda and Komai (1958); Roy *et al.* (1971); and Syouji (1981) might have resulted from a pH effect because these researchers used Ca or Na silicates as a Si source, which is known to increase soil pH. However, the maximum adsorption of Si usually occurs in the pH range of 9-10, and P in the pH range of 2-4 (Obihara and Russell 1971; Higashi and Shinagawa 1981; Imai 1981). Acid soils deficient in P usually have a pH below 5. It can be assumed that P adsorption by these soils is much great than Si adsorption. On the other hand, Toth (1939) indicated that P was released from the adsorbed state only in slightly alkaline media, meaning that displacement of P was by hydroxyl or silicate ions rather than silicic acid.

Thus it seems impossible that Si affects P availability in these soils, although further study will be necessary to confirm this speculation.

Our results suggest that increased shoot dry weight may result from other reasons. As reported in the section 1 of this chapter, P utilization in the plant might be indirectly improved by Si when the P level in solution was low. The plant P/Mn and P/Fe ratios were used as an indication of P nutrition rather than P concentration. In this experiment, as shown in Table 22, the concentration of Mn decreased with +Si. This result is in agreement with that obtained in the section 1. Although rice plants contained higher Mn especially under flooded condition, the concentration is below the critical value which is 7,000 ppm reported by Cheng and Quallete (1971). In addition, no symptoms of Mn toxicity were observed during the period of experiment. So it can say that the increased growth did not result from alleviating Mn toxicity by Si. The Si effect seems to be attributed to a higher P/Mn ratio within plants, though the P/Fe ratio did not increase. Rice is known to be an Mn-accumulator, and may contain 20 to 30 times more Mn than Fe (Table 22). Thus Mn is thought to be the main factor controlling P availability within the plant.

In summary, Si, as silicic acid, did not increase P availability in Yakuno soil. But increased shoot growth may be attributed to an indirect improvement in P utilization by the plant from a decrease in Mn uptake.

### Section 3 Effect of silicate on P availability for rice plant in a P-deficient soil

Silicate application to soils not only supply Si, but also increase soil pH. Both may produce beneficial effects on the growth of plants especially grown in acid soils deficient in P. The Si effect has been discussed in the above section, when Si was added as silicic acid to a P-deficient soil. In this section, the pH effect caused by silicate application on P availability and plant growth, which is often ignored in many cases (Fisher 1929, Silva 1971, Roy et al. 1971, and Syouji 1981), are discussed.

### MATERIALS AND METHODS

The same soil as above, Yakuno soil was used. Main treatments of flooded and nonflooded conditions with following soil subtreatments; 1. control (C), 2. sodium carbonate application (SC) and 3. sodium silicate application (SS) at 0.47 mg Si or 1 mg SiO<sub>2</sub> g<sup>-1</sup> soil, were designed. The soil pH increased to 5.5 after SS application. The soil pH with SC was adjusted to the same as that with SS. Rice plants were cultured in the above treatment soil with 4 replications. The culture methods were the same as those described in the above section. No fertilizer was applied. One month after sowing, the rice plant was harvested for analysis. The concentrations of P, Si, N, Fe and Mn in the shoots were analyzed using the methods described above.

For P adsorption experiment, the same soil samples, which were used in rice culture described above, were equilibrated with 12 mM P solution. The detailed procedures were shown in the above section. P desorption experiment was carried out on the soil samples which had previously received P (4 mg P g<sup>-1</sup> soil as Ca(H<sub>2</sub>PO<sub>4</sub>)<sub>2</sub>) or not. The soil samples were equilibrated with a range of Si concentrations as sodium silicate as indicated in the figure. The procedures were the same as those described above except that 0.1 M NaCl was used as supporting electrolyte instead of 0.01 M CaCl<sub>2</sub>. Si adsorption was measured simultaneously.

## RESULTS

SS and SC caused the soil pH (H<sub>2</sub>O) to increase by about 1 unit. SC increased shoot dry weight 6 percent under the nonflooded condition and 26 percent under flooded condition (Fig. 21). SS increased shoot dry weight more (19 and 46 percent under nonflooded and flooded conditions, respectively). Either SC or SS did not significantly increase P concentration in the shoots under both conditions (Table 24). Compared to control, SS increased the Si concentration in the shoots and decreased the Mn concentration significantly, but SC did not. The Fe concentration was less affected by SS or SC. Both SS and SC increased N concentration nearly 2 times. Compared to control, SS increased the P/Mn ratio in shoots 40 percent under nonflooded and 35 percent under flooded conditions, but SC did not.

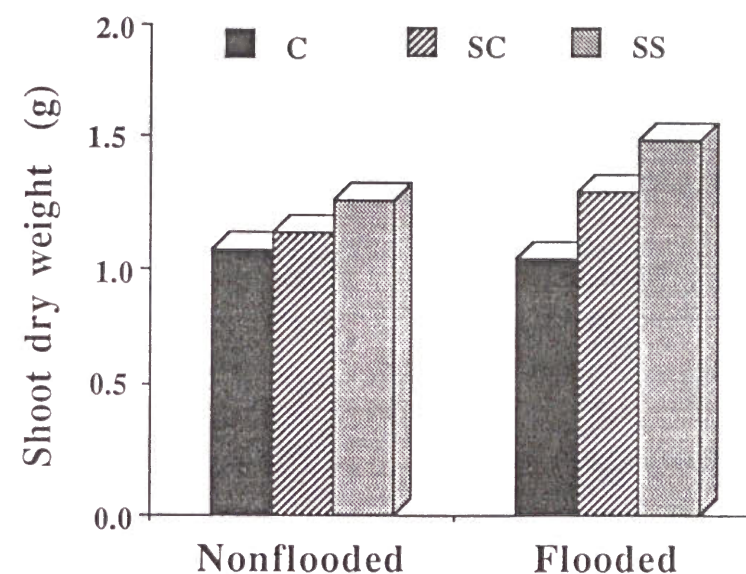


Fig. 21 Dry weight of shoots grown under different treatments. C, SC and SS represent treatments of control, sodium carbonate and silicate application, respectively. Vertical lines on bars represent SD.

P adsorption by the soil was about 170  $\mu\text{mol g}^{-1}$  soil, and was not decreased by either SS or SC (Table 25). A range of concentrations of sodium silicate did not desorb P in the soil samples which had previously received either P or not (Fig. 22). Si adsorption increased with increasing Si concentrations in the solution (Fig. 23). Si adsorption by soils was decreased by the previous application of P to the soil. The Si adsorption ranged from -35 to +720 $\times 10^{-2}$   $\mu\text{mol g}^{-1}$  soil in samples which had previously received no P, and from -50 to +470 $\times 10^{-2}$   $\mu\text{mol g}^{-1}$  soil in samples which had previously



received P.

Table 24 Elemental concentration in shoots under different treatment. Values are the mean (n=4) with SD within brackets below.

Treatment <sup>a</sup>	Nonflooded condition			Flooded condition		
	C	SC	SS	C	SC	SS
Si (%)	1.57 (0.04)	1.24 (0.07)	2.62 (0.12)	1.98 (0.05)	1.61 (0.05)	2.88 (0.08)
P (ppm)	1141 (47)	1064 (24)	1088 (37)	1250 (53)	1236 (42)	1365 (110)
N (%)	2.41 (0.07)	3.97 (0.05)	4.00 (0.12)	2.09 (0.02)	4.35 (0.03)	4.37 (0.10)
Mn (ppm)	2152 (135)	2314 (234)	1473 (275)	3715 (231)	3836 (349)	2949 (167)
Fe (ppm)	62.4 (3.7)	66.7 (2.2)	63.9 (2.4)	89.2 (4.3)	98.9 (10.6)	91.9 (3.2)
P/Mn	0.53 (0.02)	0.46 (0.04)	0.74 (0.17)	0.34 (0.01)	0.32 (0.02)	0.46 (0.03)
P/Fe	18.3 (1.70)	16.0 (0.39)	17.0 (0.94)	14.0 (0.69)	12.5 (1.04)	14.9 (0.93)

<sup>a</sup> C, SC and SS represent treatments of control, sodium carbonate and silicate application, respectively.

Table 25 P adsorption by soil samples which had previously received non (C), sodium carbonate (SC), and sodium silicate (SS). Values are means (n=3) with SD within parenthesis.

Treatment	P adsorbed ( $\mu$ mol g <sup>-1</sup> soil)
C	171.1 (0.19)
SC	172.1 (0.52)
SS	169.3 (1.24)

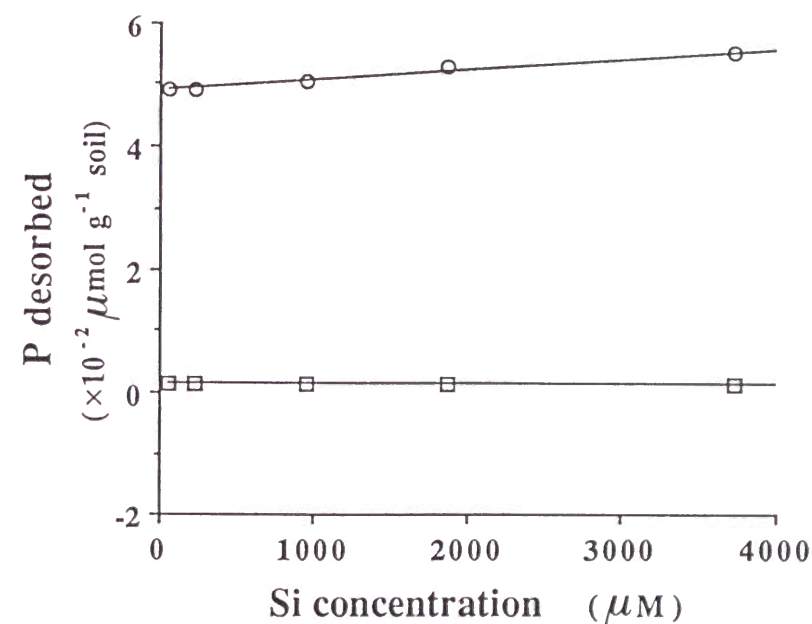


Fig. 22 Effect of Si (as silicate) concentration on P desorption in soil samples which had previously received 0 (□) or 4 mg P g<sup>-1</sup> soil (○).

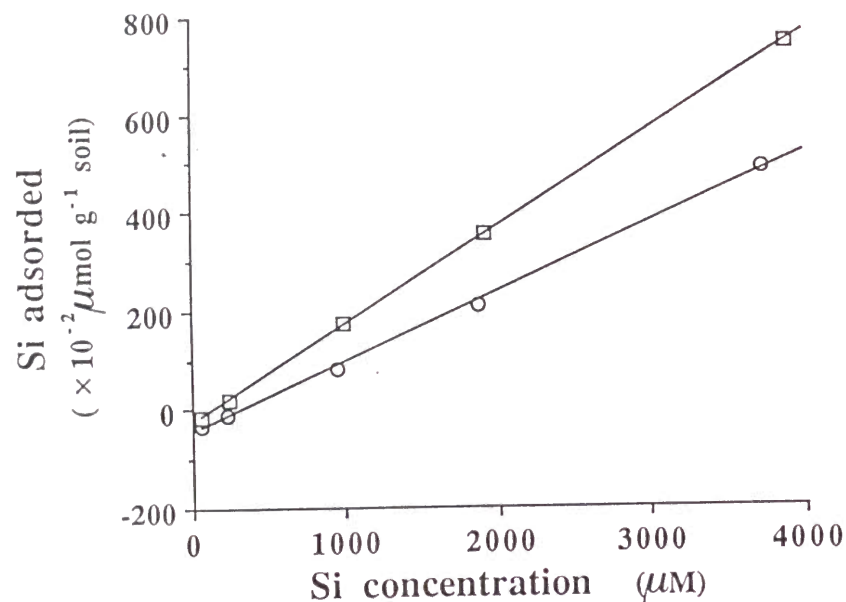


Fig. 23 Si (as silicate) adsorption by soil samples which had previously received 0 (□) or 4 mg P g<sup>-1</sup> soil (○).

## DISCUSSION

Sodium carbonate application was used as a pH control in this experiment. Shoot dry weight increased not only with SS, but also with SC under both nonflooded and flooded conditions (Fig. 21). However, SS increased the dry weight more than SC. This result shows that the beneficial effect of silicate may result from two; pH effect and Si effect. However, these effects were not accompanied by an increase in P concentration of shoots. It suggests that either

Si effect or pH effect did not result from increasing P availability in Yakuno soil.

In this experiment, the pH effect is mainly attributed to an increment of nitrogen supply from the soil (Table 22). The soil used has a high content of organic matter (Miura 1986). The pH rise by SS and SC application probably stimulated the ammonification of organic nitrogen (Kai 1978).

The Si effect may be attributed to increasing Si content in shoots and decreasing Mn uptake. Higher Si content may have many beneficial effects as discussed above. A higher P/Mn ratio within plants (Table 22) might indirectly improve P utilization in the plant as discussed in the section 1.

The soil showed very high P absorption capacity (Table 23). The effect of silicate on P adsorption can also be separated into pH effect and Si effect. Although rising pH generally decrease P adsorption, this phenomenon was not found in this experiment. As stated in the above section, a high P adsorption is assigned to high Al-humus complexes in this soil. Bloom (1981) found that P adsorption by an Al-peat complex gradually increased with increasing pH within the range 3.2 to 6.0. However, in the pH range 4.7 to 6.1, the suspensions with 80, 160, and 400 μmol liter<sup>-1</sup> initial P were little affected by pH. Wada and Gunjigake (1979) indicated that Al and Fe bound with humus, unlike Al present in the allophanelike constitutes, allophane and imogolite, react with P independently of the solution pH. In this experiment, the equilibrium pH of the soil received silicate was about 5.0, and that of control was about 4.6. In the range of these pH, it seems that P adsorption was not affected by pH rise.

Both P and Si were adsorbed by the soil (Table 23 and Fig. 23). However, much more P was adsorbed than Si (as silicate), showing that the soil has a high affinity for P. Saito and Shoji (1984) also found that the soil rich in Al-humus complexes adsorbed very small amounts of Si. The fact that a previous addition of P decreased Si adsorption suggests that some adsorption sites of Si may be the same as P. Thus when silicate is added first, Si may be adsorbed on the P sites, however when P is added then, the adsorbed Si may be displaced by P because of its high affinity. As a result, silicate can not decrease P adsorption, nor can it displace adsorbed P, while P can decrease Si adsorption.

Above results revealed that the effect of silicate on P adsorption and desorption showed the same trend as that of silicic acid stated in the section 2. Si generally exists as monosilicic acid in soil solution except in alkaline soils, and is adsorbed as  $\text{Si}(\text{OH})_4$  (McKeague and Cline, 1963a and b). At present soil pH (5.5), silicate might transform into silicic acid in the soil.

From above results, it is clear that Si, as silicate, also does not affect P availability in Yakuno soil. Based on above results, I postulate possible effects of silicate on rice plants grown in a P-deficient soil as shown in Fig. 24.

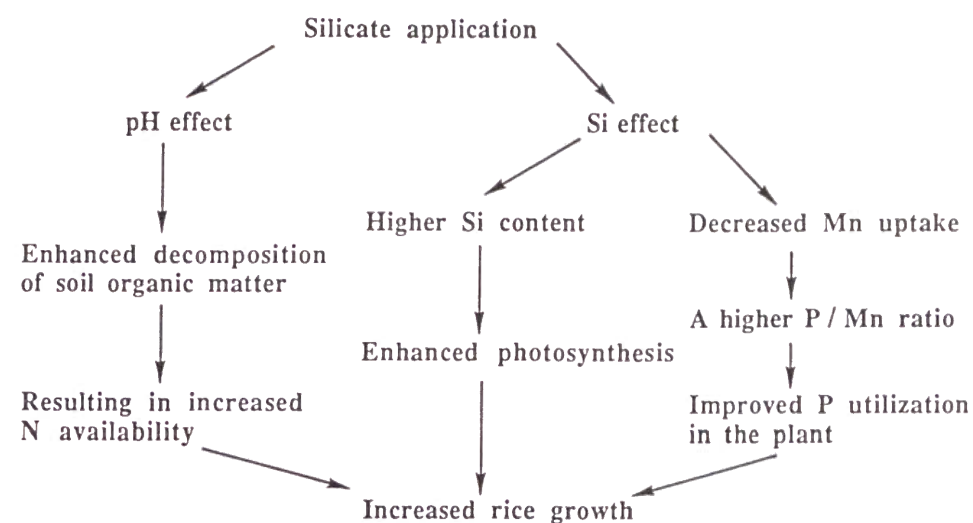


Fig. 24 Scheme for possible effects of silicate application to a P-deficient soil on rice growth.



## CHAPTER VI INTERACTION BETWEEN SILICON AND CALCIUM

As stated before, the main composition of slags is calcium silicate. When they are applied to soils, not only Si, but also Ca is supplemented as an accompanying element. Some investigations indicated that when Ca content in leaf blades was high, the formation of silica bodies was weakened (Tsuno and Higashi 1984a and b, and Tsuno and Kasahara 1984). However, as obtained in Chapter V, silicate application caused soil pH to increase, thus stimulating the ammonification of organic nitrogen. It is possible, therefore, that Ca may affect the formation of silica bodies through other factors.

On the other hand, silica bodies do not distribute uniformly in leaf blade. The histochemistry method used for detecting silica bodies can not allow one to observe extensive areas of tissues or organs. Thus this method may result in an error in calculating the number of silica bodies because of their variation. In this chapter, several experiments were conducted using water culture to clarify the interaction between Si and Ca. Soft X-ray irradiation was used for detecting silica bodies.

### MATERIALS AND METHODS

#### Effect of Si on Ca uptake by rice plants

Rice plants were cultured in the Kimura B solution with and without 100 ppm  $\text{SiO}_2$  as silicic acid using the same method as described in Chapter III. The plants were harvested for Si and Ca analysis at maturity. The content of Ca was determined by atomic absorption spectrochemical analysis after  $\text{HNO}_3\text{-HClO}_4$  digestion, and Si by the same method as described above.

#### Effect of Ca on the formation of silica bodies

Rice seedlings of 20 days age were prepared by the method described above. Three selected seedlings each were transplanted into 3 liter pots with full strength Kimura B solution in three replicates. The pots were arranged on green house tables in a completely randomized with a combination of three Ca levels and two Si levels treatments. Three Ca levels were designed as 15, 50 and 100 ppm Ca, which were supplied as  $\text{CaCl}_2$ , and two Si levels as 20 and 100 ppm  $\text{SiO}_2$  as silicic acid. The culture method was the same as described above. Two months after treatment, all plants were harvested. Si fractionation of leaf blades was conducted by the methods described in the Chapter II. The third leaf blade was used for silica body detection using Soft X-ray irradiation described in Chapter II. Four leaf blades were irradiated near 10 cm for each treatment. Silica bodies per  $1 \text{ mm}^2$  were counted 10 times on both sides of lamina midrib per each leaf blade after the films were developed and made into photographs.

## RESULTS AND DISCUSSION

The content of Ca in shoots was decreased by Si addition (Table 26). Ca uptake by -Si plants was about 30 % more than that by +Si plants, suggesting that Si decreased Ca uptake. This may result from many factors. Several experiments indicated that Ca uptake was related to transpiration. As obtained in Chapter III, Si decreased transpiration, thus partial decrease in Ca uptake may be caused by this reason. In addition, Si deposits on the root. This may affect Ca uptake through decreasing apoplastic flow and permeability of Ca, and precipitating with Ca.

Table 26 Ca content and uptake of rice shoots with and without Si

	Shoot content (%)	Uptake (mg)
+Si	0.13	155.2
-Si	0.26	197.1
+Si/-Si	0.50	0.79

Ca content of the shoots increased with increasing Ca levels in the solution (Table 27). Ca uptake was more in 20 ppm SiO<sub>2</sub> solution than in 100 ppm SiO<sub>2</sub> solution. Si content and uptake of shoots were hardly affected by Ca levels either at 20 ppm SiO<sub>2</sub> or at 100 ppm SiO<sub>2</sub>. The number of silica

bodies in 1 mm<sup>2</sup> significantly increased when rice plants were grown in 100 ppm SiO<sub>2</sub> solution compared to when those were grown in 20 ppm SiO<sub>2</sub> solution.

More than 90 % of Si was present in the form of silica gel in the leaf blade regardless of Si and Ca levels (Fig. 25). Any changes in Si forms were not found in all treatments. The significant relative coefficient was obtained between Si content and the number of silica bodies, but not between Si content and Ca content, Ca content and silica bodies (Table 28).

Table 27 Effect of Ca on Si uptake and silica body formation <sup>a</sup>

Treatment (ppm)	SiO <sub>2</sub>	20			100		
	Ca	15	50	100	15	50	100
Ca (%)		0.20	0.38	0.47	0.16	0.28	0.36
Ca uptake (mg)		20.9	38.4	47.0	15.4	31.7	39.7
Si (%)		1.49	1.44	1.57	5.30	5.34	5.31
Si uptake (mg)		153	145	157	526	597	589
Si body per 1 mm <sup>2</sup>		4.7	4.6	2.5	61.1	69.2	62.3

<sup>a</sup> The contents were those of shoots. The Si bodies were detected using the third leaf blades.

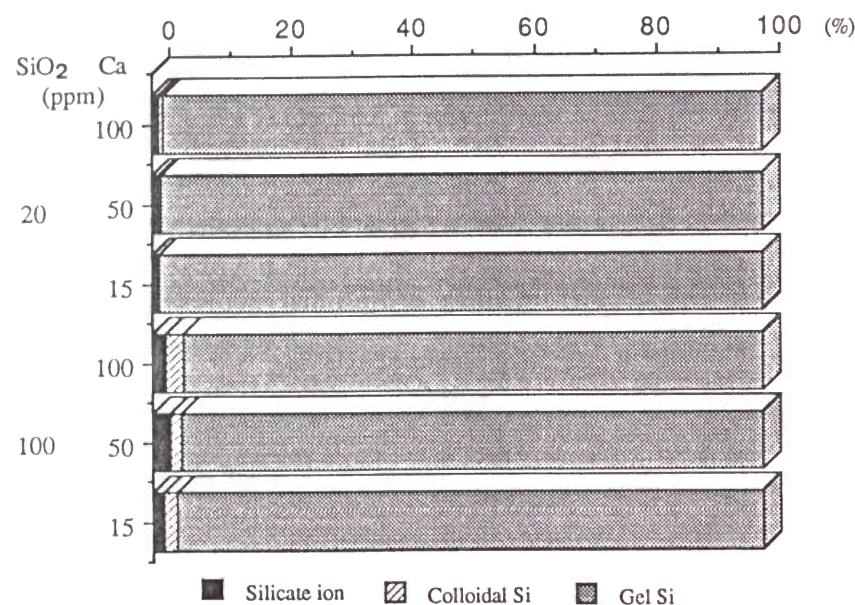


Fig. 25 Effect of Ca levels on the forms of Si in rice plants.

The effect of Ca on the formation of silica bodies was studied from three aspects; Si uptake, Si forms and silica bodies formation in leaf blade. If Ca affects the formation of silica bodies, it may result from decreasing Si uptake and affecting the transformation of ion and/or colloidal Si to gel Si in addition to weakening the formation of silica bodies. However, in this experiment neither Si uptake nor Si forms was affected when Ca content of shoots increased (Table 27).

Table 28 Relative coefficient (r) between Si content of leaf blades and silica bodies (SB) in third leaf blade, the Si content and Ca content of leaf blades, and the Ca content and the silica bodies.

	r
Si%-Ca%	-0.480
Si%-SB	+0.990**
Ca%-SB	-0.517

In the present studies, soft X-ray irradiation method was used in the detection of silica bodies. This method has many advantages compared to histochemistry method (Takeoka, Matsumura and Kaufman, 1983). One of these is that it decreases variation of silica body numbers since it can allow one to observe extensive areas of leaf blades. Using this method, the results showed that the numbers of silica bodies increased with increasing Si content of shoots, but did not change with increase in Ca content of shoot when the Si content was the same (Table 27). It suggests that the formation of silica bodies is controlled only by Si content. This result is not in agreement with that obtained in field by Tsuno and Higashi (1984a and b), Tsuno and Higashi (1984). The effect of Ca on the formation of silica bodies may be indirectly caused by other reasons in the field. Further studies should be necessary.

From the above results, it can be concluded that Si decreased Ca uptake, while Ca did not affect Si uptake, Si forms and the formation of silica bodies in



solution culture.

## CHAPTER VII AVAILABILITY OF SILICA IN RICE STRAW FOR RICE PLANTS

As stated above, rice plants accumulate Si. Takahashi (1987) estimated that nearly 20 kilogram of  $\text{SiO}_2$  is removed from the soil by rice plants for producing 100 kilogram brown rice. For satisfactory rice production, therefore, it is necessary to supplement removed Si to the soil.

Rice straw application to the soil is one of the means. Generally, it contains 4 to 20 % of  $\text{SiO}_2$  (Kawaguchi, 1978). If 5 ton straw which contains 10 %  $\text{SiO}_2$  is applied per hectare, 500 kg  $\text{SiO}_2$  will be returned to the soil. Imaizumi and Yoshida (1958) reported that about 950 kg  $\text{SiO}_2$  per ha was removed by rice plants every year, of which 70 % originated from soil, and 30 % from irrigation water. Thus 5 ton straw application will replenish about 75 % of the Si removed from the soil. However, as reported above, Si in the straw occurs mostly in the form of silica gel, while rice plants absorb Si in the form of silicic acid. Thus the transformation rate of silica gel to silicic acid determines the availability of Si in rice straw to rice plants.

Some field experiments showed that straw application either increased the Si content of rice shoots (Nakada 1980) or failed to increase it (Zhang 1984). Such discrepancies may be ascribed to the difference in the soil Si status, soil pH, Si concentration in irrigation water and experiment period.

On the other hand, rice straw application increases soil reduction. This may affect the availability of soil Si. However, it is not possible to determine the net Si release from straw only by comparing straw applied pots with non-applied ones under field conditions. This also may be the reason of the discrepancies.

In this chapter, two kinds of rice straw, Si contained or not, were prepared. The availability of Si in straw, as well as the effect of its application on the availability of soil Si were studied under non-planting and rice planting, respectively.

### Section 1 Availability of straw Si under no planting

In this section, when rice was not planted, the release of Si from rice straw was analyzed by measuring the concentration of Si in percolating water. The comparison of the effect of rice straw with and without Si on the availability of soil Si was also made.

## MATERIALS AND METHODS

The soil selected for this experiment was an alluvial soil sampled from a field in the farm attached to Kyoto University in Takatsuki. Some properties of the soil are shown in Table 29. Culture pots, 1/5000a were used for the experiment. The treatments were as follows: 1). control (3 kg soil alone); 2). 3 kg soil + 1% rice straw containing Si (referred to + Si straw later); 3). 3 kg soil

+ 1% Si-free rice straw (- Si straw). The + Si and - Si straw materials were got from rice plants cultured in the solution with and without Si in the same method as described above. Their composition is shown in Table 30. The + Si straw contained 15.5 percent of SiO<sub>2</sub>, while the - Si straw only 0.2 percent. The straw materials were cut into fragments about 1 cm before addition to soil, and mixed with soil thoroughly.

Table 29 Some properties of the soil used in the experiment.

Soil texture	pH (H <sub>2</sub> O)	CEC (meq)	Base-saturation percentage (%)
CL	6.6	11.4	70.6

Table 30 Composition of added straws

	SiO <sub>2</sub>	N	P	K	Ca	Mg
		(% )				
-Si straw	0.23	0.93	0.43	1.69	0.30	0.20
+Si straw	15.46	0.79	0.27	1.31	0.16	0.13

After the addition of the straw materials to the soil, all the treatments were flooded immediately. Water layer was maintained at 3 cm every day by addition of distilled water. Water requirement in depth per day was regarded as 1 cm, and a 3 cm water layer was removed every three days from a glass pipe with a rubber cork attached to the bottom of the pot. The SiO<sub>2</sub>

concentration in the percolating water was analyzed immediately using the colorimetric molybdenum blue method after sampling. At the end of the experiment, the amount of soil available silicate was determined by using the method of Yoshida (1958) and Takahashi (1981). The experiment was conducted in a green house during the period July 12 to September 13. Triplicates were made.

### RESULTS AND DISCUSSION

The addition of + Si straw increased the  $\text{SiO}_2$  concentration in the percolating water by 1.5 to 2 times compared with the control and - Si straw addition treatments (Fig. 26), suggesting that Si in the + Si straw was gradually released. The total amount of Si released during the experiment which was calculated from the  $\text{SiO}_2$  concentration and volume of percolating water showed that although twice as much Si as in the control was released from the + Si straw addition treatment, only about 10 percent of the Si contained in the + Si straw ( 4650 mg  $\text{SiO}_2$ ) was released (Table 31).

As obtained in CHAPTER II, less than 10 percent of Si in the rice plant was present in the form of silicate ion and colloidal silicic acid, and 90 percent or more in the form of silica gel. The small amount of Si released in this experiment suggests that only low molecular forms of Si in the + Si straw were dissolved, while silica gel remained in the soil.

Table 31 Total amount of Si released during the experiment ( $\text{SiO}_2$  mg)

Treatment	Control	-Si straw	+Si straw
	380 (100)	448 (118)	830 (218)

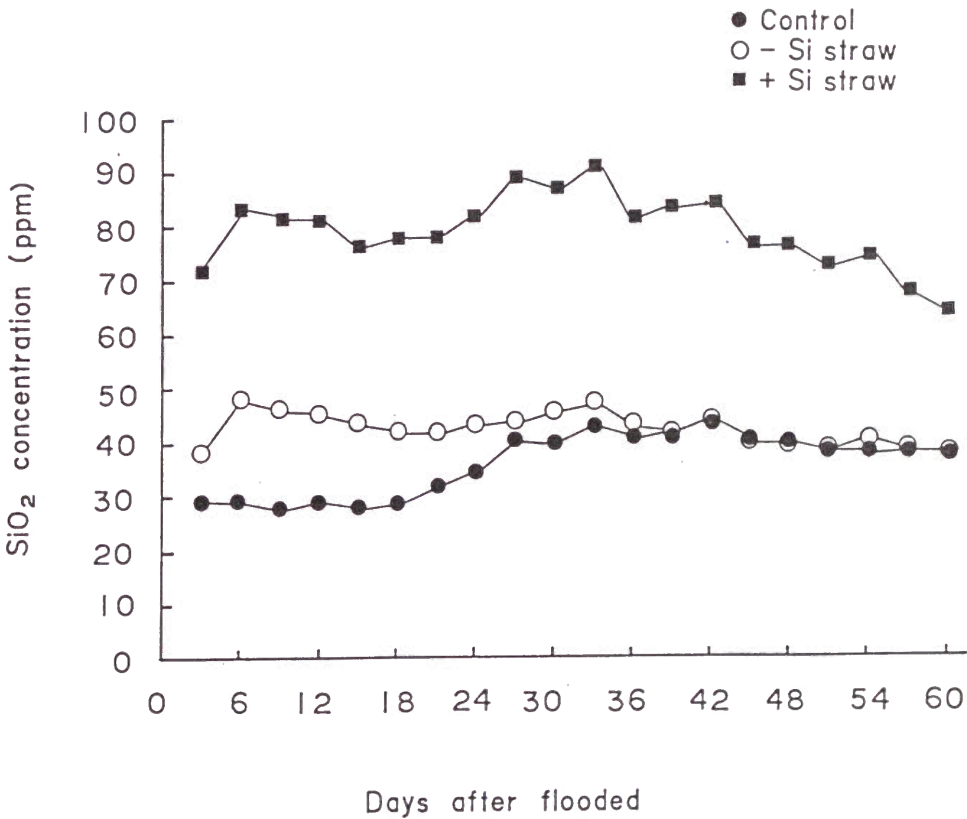


Fig. 26 Changes of  $\text{SiO}_2$  concentration in the percolation water.

Compared with the control, the -Si straw addition also increased the SiO<sub>2</sub> concentration in the percolating water to some extent until 5 weeks after flooding though the values became similar thereafter (Fig. 26). The total release from -Si straw addition treatment was increased by 18 % (Table 31). Takahashi (1981) reported that the amount of water soluble Si increased with the development of reduction in the flooded soils. Straw addition to the soil is known to increase the soil reduction because it supplies energy source for soil microorganisms, and stimulates their activity. It is suggested that the increase in the amount of Si released resulted from the solubilization of the soil Si due to the increase of the soil reduction. Therefore the amount of Si released from +Si straw originated from two sources: from the Si contained in the straw, and from increased soil available silicate. In this experiment, as shown in Table 31, the former accounted for 8 % of the Si released, and the latter for 2 %.

The amount of soil available silicate determined by the method of Yoshida at the end of the experiment was nearly 2 times that by the method of Takahashi (Table 32). This result is in agreement with that reported by Tamori (1985) and Takahashi (1986). The addition of either +Si straw or -Si straw did not affect the amount of available silicate extracted by the Yoshida method, suggesting that Si in the straw can not be extracted by acetate buffer. Zhang (1984) also reported that Si in rice straw could not be extracted by acetate buffer at pH 4, but by dilute NaOH to some extent. He found that the amount of available soil silicate at pH 5.6 was also not increased by the addition of rice straw. The amount of available silicate determined by the Takahashi

method, however, increased by 36% after the addition of +Si straw but not after that of -Si straw. This fact suggests that Si in the straw can be extracted by the Takahashi method to some extent. This result is consistent with that shown in Fig. 26.

*Table 32* Soil available silicate ( SiO<sub>2</sub> mg/100 g soil) under different treatments determined at the end of the experiment. Figures in the parentheses are the relative values of control (100).

Treatment	Determined by	
	Yoshida method	Takahashi Method
Control	31.9 (100)	14.7 (100)
-Si straw	31.0 (97)	15.1 (103)
+Si straw	33.4 (105)	20.0 (136)

Based on the results obtained, it can be concluded that the release of Si from the +Si straw was small during a short period when rice plant was not planted. The soil reduction enhanced by the straw decomposition also made soil Si available during a short period though its effect was limited.

## Section 2 Availability of straw Si under rice planting

Rice plants actively absorb Si. When rice plants were grown as a strong sink,



the availability of Si in the straw was studied in this section.

## MATERIALS AND METHODS

### First cultivation

The pot soil used in the above experiment was put for nearly one year, and then used for this experiment. The treatment design was the same as described in the section 1. Twenty-five soaked rice seeds (*Oryza sativa* L. cv. Akebono) were sown in each pot on April 19. Pot soil was kept in a water-saturated state until seedling establishment. After one week, the seedlings were thinned to 15 per pot and the soil was flooded. Three replicates of each treatment were arranged on green house tables in a completely randomized design. Plants were grown for two months after sowing in a green house, and then harvested on June 20. Dry weight and Si content of the shoots were determined. Content of soil available silicate was determined before and after cultivation using the method of Takahashi (1981). Fertilizers were applied at the rate of 1-1-1 g N-P<sub>2</sub>O<sub>5</sub>-K<sub>2</sub>O per pot before sowing. Each pot was subjected to topdressing of 0.3 g N on June 4. Sources of NPK were (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub>, NaH<sub>2</sub>PO<sub>4</sub>, and KCl.

Surface water depth was maintained at 3 cm with distilled water supplied daily. The percolating water was collected every three days and the Si concentration was determined immediately according to the method described above.

### Second cultivation

At about 5 months after the first harvest, 5 seedlings each which was sown on September 17, were transplanted to the above pots on October 14. The rice plants were put in a green house with a heater and supplementary light, and harvested on December 18. The Si concentration in the percolating water and the content of soil available silicate were determined only before transplanting. Nitrogen, P and K were applied before transplanting at the same rate as in the first cultivation.

### Successive extractions

To examine the solubility of Si in the straw, the Si was successively extracted by distilled water. The method was the same as that for soil available silicate proposed by Takahashi (1981). Two replicates each of 1 g sample of ball milled straw powder containing 15.5 % SiO<sub>2</sub> were equilibrated with 60 ml of distilled water in 100-ml plastic bottles. The test solution was kept at a constant temperature of 40°C for 1 week, and then filtered. The Si in filtrate was analyzed by the method described above, and the residue was re-extracted by using the procedures described above. The extraction was carried out 10 times.

## RESULTS AND DISCUSSION

In the first cultivation, the +Si straw treatment increased the SiO<sub>2</sub>

concentration in the percolating water by 5 to 10 ppm during the first two weeks after flooded, compared to the control and the -Si straw treatment (Fig. 27). However, the  $\text{SiO}_2$  concentrations reached to the same level thereafter. In contrast to the case in which rice plant was not planted (Fig. 26), the  $\text{SiO}_2$  concentration in the percolating water significantly decreased with the progression of rice growth. This fact suggests that rice plant has a strong ability to take up Si. The -Si straw treatment did not affect the  $\text{SiO}_2$  concentration.

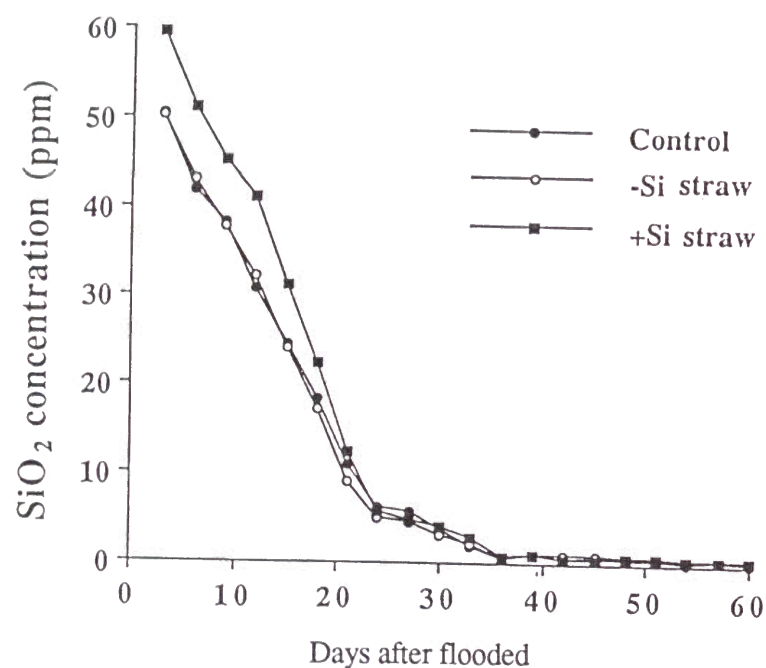


Fig. 27 Changes of  $\text{SiO}_2$  concentration in the percolating water with the progression of rice growth under different treatments (first cultivation).

Table 33 Estimated leaching loss of Si during the experiment ( $\text{SiO}_2$  mg/pot) <sup>a</sup> (first cultivation).

Treatment	Control	-Si straw	+Si straw
	202	198	237

<sup>a</sup> Calculated from the  $\text{SiO}_2$  concentration in the percolating water and the volume of percolating water.

Table 33 shows the estimated leaching loss of Si (calculated from the  $\text{SiO}_2$  concentration and the volume of percolating water). The values were much lower than those when rice was not planted as shown in the section 1, suggesting that the Si uptake by rice plants reduced the leaching loss of Si. The amount of Si that leached out was about 20 % more in the +Si straw treatment compared with the control and the -Si straw treatment. The +Si straw treatment significantly increased the Si content in the shoots although it did not significantly increase the dry weight of the shoots (Table 34). Si uptake by rice plants from the +Si straw treatment was 25% and 22% more than that from the control and the -Si straw treatment, respectively. About 80% of the Si absorbed by rice plants originated from the soil, and 20% of the Si originated from the added +Si straw, while only 6% of the Si contained in the added +Si straw was released.

*Table 34* Shoot dry weight , Si content and Si uptake under different treatments (first cultivation). Values are means (n=3) with SD within parentheses.

Treatment	Dry weight (g/pot)	Si content (SiO <sub>2</sub> %)	Si uptake (SiO <sub>2</sub> mg/pot)
Control	21.49 (1.24)	3.84 (0.09)	826.2 (56.0)
-Si straw	22.02 (1.27)	3.86 (0.22)	848.7 (32.1)
+Si straw	23.30 (0.89)	4.44 (0.11)	1033.8 (25.5)

With the +Si straw, the amount of soil available silicate extracted by the Takahashi method increased by 15 % before cultivation and 10 % after cultivation, respectively (Table 35). The content of soil available silicate decreased after cultivation, which is in agreement with the findings reported by Tamori (1985) and Takahashi (1986).

*Table 35* Content of soil available silicate determined before and after cultivation under different treatments (first cultivation). Values are means (n=3) with SD within parentheses <sup>a</sup>.

Treatment	Before cultivation	After cultivation
(SiO <sub>2</sub> mg/100 g soil)		
Control	16.7 (1.0)	13.8 (0.8)
-Si straw	16.2 (0.7)	13.8 (0.4)
+Si straw	19.2 (0.9)	15.2 (0.6)

<sup>a</sup> Content of soil available silicate was determined by the method of Takahashi.

In the second cultivation, the Si concentration in the percolating water and the content of soil available silicate increased (Table 36), compared to the end of the first cultivation although the concentration could not completely return to the initial levels (Table 35 and Fig. 27). The dry weight of the control decreased for unknown reasons, but compared to the -Si straw treatment, the Si content of the shoots and Si uptake increased with the +Si straw treatment. However, only about 3% of the Si contained in the added straw was absorbed by the rice plants.

*Table 36* Content of soil available silicate (SAS SiO<sub>2</sub> mg/100 g soil) and Si concentration in the percolating water (SPW SiO<sub>2</sub> ppm) before cultivation, and shoot dry weight, Si content and Si uptake under different treatments (second cultivation). Values are means (n=3) with SD within parentheses.

Treatment	Before cultivation		Dry weight (g/pot)	Si content (SiO <sub>2</sub> %)	Si uptake (SiO <sub>2</sub> mg/pot)
	SAS	SPW			
Control	15.1 (0.2)	39.2 (0.2)	6.18 (0.03)	7.14 (0.08)	441.2 (3)
-Si straw	15.5 (1.4)	37.9 (0.6)	8.97 (0.02)	5.50 (0.15)	429.7 (13.9)
+Si straw	17.3 (0.2)	43.3 (1.7)	9.31 (0.04)	6.46 (0.01)	601.4 (1.65)

The above facts suggest that the availability of Si in the +Si straw was low. Based on the results of a long-term field experiment covering a period of 40 years which was conducted at Shiga Agricultural Station (Nakada 1980), Takahashi (1987) estimated that about 70 percent of the Si contained in the compost was utilized by the crops (rice as first crop and wheat as second crop). This value was much higher than that obtained in this experiment (lower than 10 %). The higher utilization of Si in the compost may be due to the difference in the method of calculation as the total uptake of 40 years was

computed by the author. Thus accumulative effect of 40 years resulted in a high value.

Zhang (1984) added straw contained 8.6 % as SiO<sub>2</sub> at different rate to two soils differing in the pH value. Three months after flooding, he measured the Si concentration in the solution, and found that Si released from the straw was about 0.5 % in the soil with pH 5.6 and 20 % in the soil with pH 7.3 regardless of the added rate. A field experiment indicated that straw application at the rate of 4500 Kg per hectare to an acid soil increased the content of soil available silicate only by about 10 %. He also reported that about 45 % of the Si in the straw could be extracted by 0.025 N NaOH, but not by acetate buffer (pH 4). These facts suggest that Si in the straw can be dissolved in an alkaline environment. However, in acid soils, which are generally deficient in available Si, the Si release from straw is low during a short period (one year or one crop) compared to the added amount although the soil available Si and shoot Si content increased some. The application of Si materials that are more available such as slags in these acid soils may be desirable for satisfactory growth of rice plants.

The -Si straw treatment did not affect either the Si content in the shoot or Si uptake by rice plants (Tables 34 and 35). This fact suggests that the effect of the increased soil reduction caused by straw application on the availability of soil Si is time-dependent.

The solubility of Si in the straw which was about 100 ppm SiO<sub>2</sub> in the first two extractions, decreased to about 40 ppm SiO<sub>2</sub> (Fig. 28). The solubility



in the latter extractions fluctuated at around 40 ppm  $\text{SiO}_2$ . As stated above, less than 10 % of Si in rice plants was present in the form of silicate ion and colloidal silicic acid. Since the straw was dried before use, the form of Si may have changed, but the increase in the Si release during the first two extractions (4.1 and 3.6 %, respectively) suggested that Si may have originated from the form with low polymerization. Yoshida (1962, 1963) found that the solubility of rice Si in hot water was the same as that of silica gel and was much higher than that of opal and diatomaceous earth. Based on infrared absorption studies, he concluded that silica gel accounted for 90 % or more of Si in rice plants. However, Wilding and Hallmark (1979), Bartoli and Wilding (1980) studied the dissolution of biogenic opal of forest and grass origin, and found that the solubility under natural conditions was very low, approaching that of geological opal and quartz. They suggested that biogenic opal was not sufficiently labile under most soil environments to account for the observed soluble Si level. In our experiment, the solubility was intermediate between that of the silica gel and opal.

Alexander (1967) indicated that the dissolution of amorphous silica depended on the particle size. The dissolution of small particles was higher than that of large ones. The silica originating from different plants may differ in size. On the other hand, since the silica in the plants is wrapped by organic matter, its release may be affected. In addition, the water content of silica from different origins may be different, and even if silica is derived from the same origin, the water content of the sample used may be different depending upon

air-dried or ashed, while the dissolution of silica is affected by hydration. Therefore a simple comparison with chemical reagents can not be made. Further studies on the properties of Si in plants should be carried out.

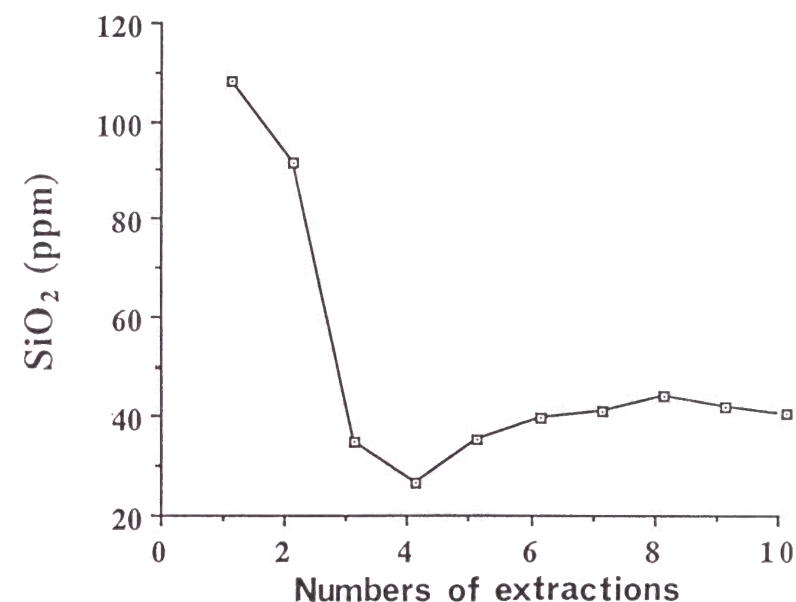


Fig. 28 Successive water extractions of Si in the +Si straw.

## CONCLUSIONS

I investigated the beneficial effects of Si in rice plants from direct and indirect aspects, and found that the direct effects reflect in promoting photosynthesis, and indirect effects in balancing nutrient uptake. The main detailed results were obtained as follows:

1. Silica gel is the most important form of Si in rice plant. Its deposition process in leaf blades is from silica cell to silica bodies with increasing Si content of shoots. Below 5 %  $\text{SiO}_2$  in shoots, cells are also silicified, but silica bodies hardly formed
2. Si effects have the characteristics of accumulation. Its effect can not be detected during a short time. Si deposited in leaf blades may promote the photosynthesis by reducing water stress, improving light transmission and light-receiving forms. Si deposited in hull increases the percentage of filled spikelets by reducing excess water loss.
3. Si effect on dry matter and yield productions is most remarkable during the reproductive stage. During this stage, rice plants absorb large amount of Si, moreover, accumulate it in leaf blades, especially in flag leaf.
4. The interaction between Si and P is not direct, but indirect. In water culture, when P is low, Si cause a decrease in Fe and Mn uptake and thus promote P availability within plant. When P is high, Si reduce P uptake and thus decrease inorganic P concentration in shoots. In soil culture, neither silicic acid nor silicate affect P availability in a P-deficient soil, but decreased Mn uptake

indirectly improves P utilization in the plants.

5. Si decreases Ca uptake, but the reverse is not true. Ca does not affect Si forms in the plants and silica bodies formation.
6. The availability of Si in the straw is low during short term. The application of materials with a higher availability of Si may be desirable for satisfactory growth of rice plants.

## REFERENCES

- Alexander, G. (1967) *Silica and Me*, Doubleday & Company, Inc.
- Bartoli, F. and Wildiing, L. P. (1980) Dissolution of biogenic opals as a function of its physical and chemical properties. *Soil Sci. Soc. Am. J.*, **44**, 873-878.
- Bastisse, E. M. (1947) Recherches sur les conditions theoriques et pratiques permettant le maintien de l'assimilabilite de l'acide phosphorique dans les terres lateritiques. *Ann. Agron.* **16**, 463-475.
- Biddulph, O. (1953) Translocation of radioactive mineral nutrients in plant. *Kan. Agr. Exp. Sta. Rep.* **4**, 48-58.
- Bloom, P. R. (1981) Phosphorus adsorption by an aluminum-peat complex. *Soil Sci. Soc. Am. J.*, **45**, 267-272.
- Bortner, C. E. (1935) Toxicity of manganese to turkish tobacco in acid Kentucky soils. *Soil Sci.* **39**, 15-33.
- Brenchley, W. E., Maskell, E. J. and Warington, K. (1927) The inter-relation between Si and other elements in plant nutrition. *Ann. Appl. Biol.* **xiv**, 45-82.
- Cheng, B. T. and Quellette, G. J. (1971) Manganese availability in soil. *Soils Fert.* **34**, 589-595.
- Committee on the methods of crop analysis (1982) Methods of phosphate analysis. *In Methods of Cultured Plant Analysis*. pp 344-348. Yokendo

publishers, Tokyo, Japan.

- Fisher, A. R. (1929) A preliminary note on the effect of sodium silicate in increasing the yield of barley. *J. Agric. Sci.* **19**, 132-139.
- Gile, P. L. and Smith, J. G. (1925) Colloidal silica and efficiency of phosphorus. *J. Agric. Res.* **xxxi**, 247-260.
- Hall, A. D. and Morison, C. G. T. (1906) On the function of silica in the nutrition of cereals-part I, *Proc. Roy. Soc.* **77**, 455-477.
- Hatamoto, K. (1987) Method for measuring photosynthesis and transpiration rate. *Shimazu Review*, **44**, 65-69.
- Higashi, T. and Shinagawa, A. (1981) Phosphorus sorption by Al(Fe)-humus complexes in volcanic ash soils. *Mem. Fac. Agr. Kagoshima Univ.* **17**, 253-258.
- Hirasawa, T., Iida, Y. and Ishihara, K. (1989) Dominant factors in reduction of photosynthetic rate affected by air humidity and leaf water potential in rice plants. *Japan. Jour. Crop Sci.*, **58**, 383-389.
- Imai, H. (1981) Effect of equilibrium pH on P adsorption by andosols. *Jpn. Soil Sci. Plant Nutr.* **52**, 11-19.
- Imaizumi, K. and Yoshida, S. (1958) Studies on Si supply of paddy soil. *Bull. Jpn. Agric. Tech. Inst.*, **B8**, 261-304.
- Ishihara, K. and Saitoh, K. (1987) Diurnal courses of photosynthesis, transpiration, and diffusive conductance in the single-leaf of the rice plants grown in the paddy field under submerged condition. *Japan. Jour. Crop Sci.*, **56**, 8-17.

- Ishizuka, K. Koike, Z. *et al.* (1958) Effect of Si on the growth and yield of rice under different nitrogen levels. *In: Studies on maximizing the yield of agricultural products by the application of silicate materials.* Monbusho, Tokyo, pp. 5-12.
- Kai, H. (1978) Fertility in paddy soil. *In Paddy Soil Science.* (eds) Kawaguchi, K. pp 229-242. Kodansha Publishers, Tokyo.
- Kaufman, P. B., Takeoka, Y., Carlson, T. J. *et al.* (1979) Studies on silica deposition in sugarcane using scanning electron microscopy, energy-dispersive X-ray analysis, neutron activation analysis and light microscopy. *Phytomorphology*, **29**, 185-193.
- Kawamitsu, M., Kawamitsu, Y., Agata, W. and Kaufman, P. B. (1989) Effect of SiO<sub>2</sub> on CO<sub>2</sub> assimilation rate, transpiration rate, leaf conductance and dry matter production in rice plants. *Sci. Bull. Fac. Agr., Kyushu Univ.*, **43**, 161-169.
- Kundu, S., Kamath, M. B. and Goswami, N. N. (1988) Effect of sulfate, silicate and fluoride anions-I, Phosphate fixation in soil. *J. Indian Soc. Soil Sci.* **36**, 43-47.
- Laws, W. D. (1951) Water-soluble silicate application to a calcareous clay soil and effect on soil properties and nutrient uptake by plants. *Proc. Soil Sci. Soc. Am.* **15**, 89-92
- Lemmermann, O. and Wiessmann, H. (1922) Die ertragssteigernde Wirkung der Kieselsäure bei unzureichender Phosphorsäureernährung der Pflanzen. *Z. Pflanzenernähr. Düng. (A)* **1**, 186-255.

- Ma, J. F. and Takahashi, E. (1989) Effect of silicic acid on phosphorus uptake by rice plant. *Soil Sci. Plant Nutr.* **35**, 227-234.
- Matoh, T., Kairusmee, P. and Takahashi, E. (1986) Salt-induced damage to rice plants and alleviation effect of silicate. *Soil Sci. Plant Nutr.*, **32**, 295-304.
- Matsushima, S. (1957) Studies on yield principle in rice plants and its application. *Bull. Natl. Inst. Agric. Sci. (Tokyo)*, **A5**, 1-271.
- McKeague, J. A. and Cline, M. G. (1963a) Silica in soil solution. I. The form and concentration of dissolved silica in aqueous extracts of some soils. *Can. J. Soil Sci.*, **43**, 71-82.
- McKeague, J. A. and Cline, M. G. (1963b) Silica in soil solution. II. The adsorption of monosilicic acid by soil and by other substances. *Can. J. Soil Sci.*, **43**, 83-96.
- Mitani, S. and Takato, H. (1960) Nutritional significance of Si in crops. I. Si deficient culture of rice plant and its symptoms. *J. Sci. Soil Manure, Jpn*, **30**, 55-539.
- Miura, K. (1986) Genesis of soils derived from various types of parent rock in southwestern Japan. Doctor thesis, Kyoto University.
- Murata, Y. (1961) Studies on the photosynthesis of rice plant and culture significance. *Bull. Natl. Inst. Agric. Sci. (Tokyo)*, **D 9**, 1-169.
- Nakada, H. (1980) Mathematical statistics analysis of the influence of long term application of three nutrient elements and compost on low land productivity. *Spec. Bull. Shiga Agric. Exp. Stn.*, **13**, 1-108.



- Noda, M. and Komai, Y. (1958) Effect of silicate materials on the availability of inorganic phosphate in the soil. *In* studies on the maximizing the yield of agricultural products by the application of silicate materials, pp. 100-115, Monbusho, Tokyo, Japan.
- Obihara, C. H. and Russell, E. W. (1972) Specific adsorption of silicate and phosphate by soils. *J. Soil Sci.*, **23**, 105-117.
- Okuda, A. and Takahashi, E. (1961a) Studies on the physiological role of Si in crop plants, I. Discussion on the Si deficient culture method. *J. Sci. Soil Manure, JPN*, **32**, 475-480.
- Okuda, A. and Takahashi, E. (1961b) Studies on the physiological role of Si in crop plants, II. Effect of the period of Si deficiency on the growth of rice plant and nutrients uptake. *J. Sci. Soil Manure, Jpn*, **32**, 481-488.
- Okuda, A. and Takahashi, E. (1962a) Studies on the physiological role of Si in crop plants, V. Effect of Si on the excess damage of iron, manganese, copper, aluminum, cobalt and arsenic in rice and wheat. *J. Sci. Soil Manure, Jpn*, **33**, 1-8.
- Okuda, A. and Takahashi, E. (1962b) Studies on the physiological role of Si in crop plants, VI. Effect of Si on the oxidation power of root and iron uptake. *J. Sci. Soil Manure, Jpn*, **33**, 59-64.
- Okuda, A. and Takahashi, E. (1962c) Studies on the physiological role of Si in crop plants, VII. Effect of Si on rice growth at different phosphorus levels. *J. Sci. Soil Manure, Jpn*, **33**, 65-69.
- Okuda, A. and Takahashi, E. (1962d) Studies on the physiological role of Si

- in crop plants, VIII. Specificity of Si uptake by rice plants. *J. Sci. Soil Manure, Jpn*, **33**, 217-221.
- Parry, D. W. and Soni, S. L. (1972) Electron-probe microanalysis of Si in the roots of *Oryza sativa* (L.). *Ann. Bot.*, **36**, 781-783.
- Rostow, E. W. (1973) Silicon. *In* Bailar, J. C., Emeleus, H. J., Nyholm, R., Trotman-Dickenson, A. F. (eds) *Comprehensive inorganic chemistry*, vol. **III**. Pergamon, New York London.
- Roy, A. C., Ali, M. Y., Fox, R. L. and Silva, J. A. (1971) Influence of calcium silicate on phosphate solubility and availability in Hawaiian Latosols. *Proc. Int. Symp. Soil Fert. Eval. (New Delhi)* **1**, 757-765.
- Sachs, J. (1862) Ergebnisse einiger neuerer Untersuchungen über die in Pflanzen enthaltene Kieselsäure. *Flora*, **33**, 65-71.
- Saito, K. and Shoji, S. (1984) Silica adsorption and dissolution properties of andosols from northeastern Japan as related to their noncrystalline clay mineralogical composition. *Soil Sci.*, **138**, 341-354.
- Seo, S. W. and Ota, Y. (1981) Role of the hull in the ripening of rice plant. I. Changes in the content in mineral elements of the hull during ripening. *Japan. Jour. Crop Sci.*, **51**, 97-104.
- Seo, S. W. and Ota, Y. (1982a) Role of the hull in the ripening of rice plant. II. Changes in photosynthesis and respiration of hull during ripening. *Japan. Jour. Crop Sci.*, **51**, 105-109.
- Seo, S. W. and Ota, Y. (1982b) Role of the hull in the ripening of rice plant. III. Localization of Si, P, K and Ca in hull. *Japan. Jour. Crop Sci.*, **51**,

349-353.

- Seo, S. W. and Ota, Y. (1982c) Role of the hull in the ripening of rice plant. V. Water loss in hull and development of rice kernel. *Japan. Jour. Crop Sci.*, **51**, 529-534.
- Shoji, S. and Fujiwara, Y. (1984) Active aluminum and iron in the humus horizons of andosols from northeastern Japan: Their forms, properties, and significance in clay weathering. *Soil Sci.*, **137**, 217-226.
- Shoji, S., Ito, T., Saigusa, M., and Yamada, I. (1985) Properties of nonallophanic andosols from Japan. *Soil Sci.*, **140**, 265-277.
- Silva, J. A. (1971) Possible mechanisms for crop response to silicate applications. *Proc. Int. Symp. Soil Fert. Eval. (New Delhi)*, **1**, 805-814.
- Smyth, J. T. and Sanchez, P. A. (1980) Effects of lime, silicate, and phosphorus sorption on ion retention. *Soil Sci. Soc. Am. J.* **44**, 500-505
- Syouji, K. (1981) Application effect of calcium silicate, rice straw and citrate on availability of phosphorus in soil. *J. Sci. Soil Manure, JPN.* **52**, 253-259.
- Takahashi, E. (1966) Studies on the physiological role of Si in crop plants, 13. Effect of Si on the resistance of rice to radioactivity. *J. Sci. Soil Manure, Jpn*, **37**, 183-188.
- Takahashi, E., Arai, K. and Kashida, Y. (1966) Studies on the physiological role of Si in crop plants. 14. Effect of Si on CO<sub>2</sub> assimilation and translocation of assimilate to panicle in rice plants. *J. Sci. Soil Manure, Jpn*, **37**, 594-598.

- Takahashi, E. and Hino, K. (1978) Effect of Si forms on Si uptake by rice plants. *J. Sci. Soil Manure, Jpn*, **49**, 357-360.
- Takahashi, E. (1987) Silica accumulator. *In Silicophilous Plant and Calciphilous Plant*. Noubunkyo, Tokyo, pp. 54-103.
- Takahashi, K. (1981) Effect of slags on the growth and the Si uptake by rice plant and the available silicates in paddy soil. *Bull. Natl. Shikoku Agric. Exp. Stn.*, **38**, 75-113.
- Takahashi, K. (1986) Available silicates in paddy soils. Part 2. Development of method of measuring available silicates and its application to soil silicate analysis. *Bull. Shikoku Natl. Agric. Exp. Stn.*, **47**, 16-39.
- Takeoka, Y., Matsumura, O. and Kaufman, P. B. (1983) Studies on silicification of epidermal tissues of grasses as investigated by soft X-ray image analysis. I. On the method to detect and calculate frequency of silica bodies in bulliform cells. *Japan Jour, Crop Sci.*, **52**, 544-550.
- Tamori, Y. (1985) Effect of silicate materials and soil properties on the Si uptake by rice plant. Bachelor Thesis, Kyoto University.
- Tanaka, K. (1980) Comparative studies on Si nutrition. MSc Thesis, Kyoto University.
- Toth, S. J. (1939) The stimulating effects of silicates on plant yields in relation to anion displacement. *Soil Sci.* **47**, 123- 141.
- Tsuno, Y. and Higashi, K. (1984a) Studies on antagonism between Si and Ca in rice plants. I. Effect of wind speed and water depth of irrigation on Si and Ca content of leaf blade. *Japan. Jour, Crop Sci.*, **53**, 76-77.

- Tsuno, Y. and Higashi, K. (1984b) Studies on antagonism between Si and Ca in rice plants. II. Antagonism between the content of Ca and Si in leaf blades. Japan. Jour, Crop Sci., **53**, 78-79.
- Tsuno, Y. and Kasahara, H. (1984) Studies on antagonism between Si and Ca in rice plants. III. Effect of Si and Ca on the resistance of blast disease in field. Japan. Jour, Crop Sci., **53**, 80-81.
- Wada, K. and Gunjigake, K. (1979) Active aluminum and iron phosphate adsorption in ando soils. Soil Sci., **128**, 331-336.
- Wilding, L. P., Hallmark, C. T., and Smeck, N. E. (1979) Dissolution and stability of biogenic opal. Soil Sci. Soc. Am. J., **43**, 800-802.
- Yamazaki, T. (1966) Silicon. *In* Micro and Macro Nutrients -Diagnosis and Treatment for Soils and Crops. Hakuyusha, Tokyo, pp. 195-221.
- Yoneyama, T. (1988) Problems on phosphorus fertility in upland soil; 5. Uptake and metabolism of phosphorus of plant. Agriculture and Horticulture. **63**, 16-20.
- Yoshida, S., Ohnishi, Y. and Kitagishi, K. (1962a) Histochemistry of Si in rice plant. I. A new method for determining the localization of Si within plant tissues. Soil Sci. Plant Nutr., **8-1**, 30-35.
- Yoshida, S., Ohnishi, Y. and Kitagishi, K. (1962b) Histochemistry of Si in rice plant. II. Localization of Si within rice tissues. Soil Sci. Plant Nutr., **8-1**, 36-41.
- Yoshida, S., Ohnishi, Y. and Kitagishi, K. (1962c) Histochemistry of Si in rice tissues. III. The presence of cuticle-silica double layer in the epidermal

- tissue. Soil Sci. Plant Nutr., **8-2**, 1-5.
- Yoshida, S., Ohnishi, Y. and Kitagishi, K. (1962d) Chemical forms, mobility and deposition of Si in rice plant. Soil Sci. Plant Nutr., **8-3**, 15-21.
- Yoshida, S. (1963) Chemical aspects of the role of Si in physiology of the rice plant. Bull. Jpn. Agric. Tech. Inst., **B15**, 1-58.
- Yoshida, S. (1978) The availability of Si in paddy soil. *In* Paddy Soil Science, (eds) Kawaguchi, K., pp. 293-299. Kodansha, Tokyo.
- Zhang, H. L. (1984) Studies on soil silica. *In* Studies on Calcium and Si Fertilizers, (eds) Nanjing Institute of Soil Science, pp. 86-96, Academia Sinica Press, Nanjing.



## LIST OF PUBLICATIONS

1. Ma, J. F. and Takahashi, E. (1989) Effect of Silicic Acid on Phosphorus Uptake by Rice Plant. *Soil Sci. Plant Nutri.* **35**, 227-234.
2. Ma, J. F., Nishimura, K. and Takahashi, E. (1989) Effect of Si on the Growth of Rice Plant at Different Growth Stages. *Soil Sci. Plant Nutri.* **35**, 347-356.
3. Ma, J. F. and Takahashi, E. (1989) Release of Si from Rice Straw under Flooded Conditions. *Soil Sci. Plant Nutri.* **35**, 663-667.
4. Takahashi, E., Ma, J. F. and Miyake, Y. (1990) The Possibility of Si as an Essential Element for Higher Plants. *Comments Agric. Food Chemistry.* **2**, 99-122.
5. Ma, J. F. and Takahashi, E. (1990) Effect of Si on the Growth and Phosphorus Uptake of Rice. *Plant and Soil.* **126**, 115-119.
6. Ma, J. F. and Takahashi, E. (1990) The Effect of Silicic Acid on Rice in a P-deficient Soil. *Plant and Soil.* **126**, 121-125.
7. Ma, J. F. and Takahashi, E. (1990) The Availability of Si in Rice Straw to Rice Plant. *Soil Sci. Plant Nutri.* in press.
8. Ma, J. F. and Takahashi, E. (1990) The Effect of Silicate on Rice in a P-deficient Soil. *Plant and Soil.* in press.

## ACKNOWLEDGMENTS

I wish to thank Professor Eiichi Takahashi, Department of Agricultural Chemistry, College of Agriculture, Kyoto University, for his kind guidance and continuous encouragement in carrying out this study.

I wish to express my gratitude to Professor Yasuhito Miyake, Faculty of Agriculture, Okayama University, for his valuable advice and supplying seeds of Akebono every year.

It is a great pleasure to acknowledge Associate Professor Yoji Takeoka, Faculty of Agriculture, Nagoya University for his discussion and kind instruction in using SOFTEX.

I am grateful to Associate Professor Wang Dai Ping, Department of Soil and Agrochemistry, Nanjing Agricultural University, for his valuable discussion and help.

I am greatly indebted to Dr. Kazuhiko Watanabe, Hyogo Prefectural Institute, for his kind advice and friendship.

My sincere thanks are due to Associate Professor Michiharu Kobayashi, Dr. Kazuo Nishimura, Dr. Toru Matoh, Plant Nutrition Laboratory, Kyoto University, for their discussion and encouragement.

To the following colleagues and friends, I give my very sincere thanks: Mis. Junko Masuda, Mr. Motohiko Kondo, Dr. Kouzou Iwasaki, Dr. Hiroshi Hirotani, Dr. Masanobu Matsusita, Mr. Hirohide Sakaguchi, Mr. Ko Toyao,

Mr. Noriyuki Yoshimura, and all other members of the Plant Nutrient Laboratory, Department of Agriculture Chemistry, College of Agriculture, Kyoto University, for their encouragement, cooperation and friendship.

I greatly appreciate the Chinese Government for financial support during my study in Japan.

Finally, I want to express my deep appreciation to my parents and my wife. If there is no their spirit support and constant understanding, I can not fulfill this thesis.

December, 1990

A handwritten signature in Chinese characters, which reads '马建峰' (Ma Jianfeng). The signature is written in a cursive style with three distinct characters.

Ma Jianfeng